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FACTORS CONTROLLING FOREST SUCCESSIONS AT LAKE ITASCA, MINNESOTA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 322

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(WITH EIGHTEEN FIGURES)

Introduction

From the standpoint of vegetation, Minnesota may be divided into two great regions by a line running from the northwestern to very nearly the southeastern corner of the state. Of these, the prairie occupies the southwestern and the forest the northeastern half. The forest region is divided into a coniferous area that may be regarded as a continuation of the northern coniferous forest formation, and a deciduous area which is an extension of the central hardwoods, with a steadily decreasing number of species toward the northwest (fig. 1).

Distribution of the three climax formations

CLIMATIC FACTORS.—It has been generally recognized that the main control of the distribution of the great climax formation of prairie, coniferous forest, and deciduous forest has been determined by climate. Low precipitation combined with high evaporating power is the limiting factor in the distribution of prairies. SCHIMPER (**28**) has shown that the prairie district of the United States is determined by the amount and seasonal distribution of the precipitation. The dry winter, the uniformly moist early summer, and the

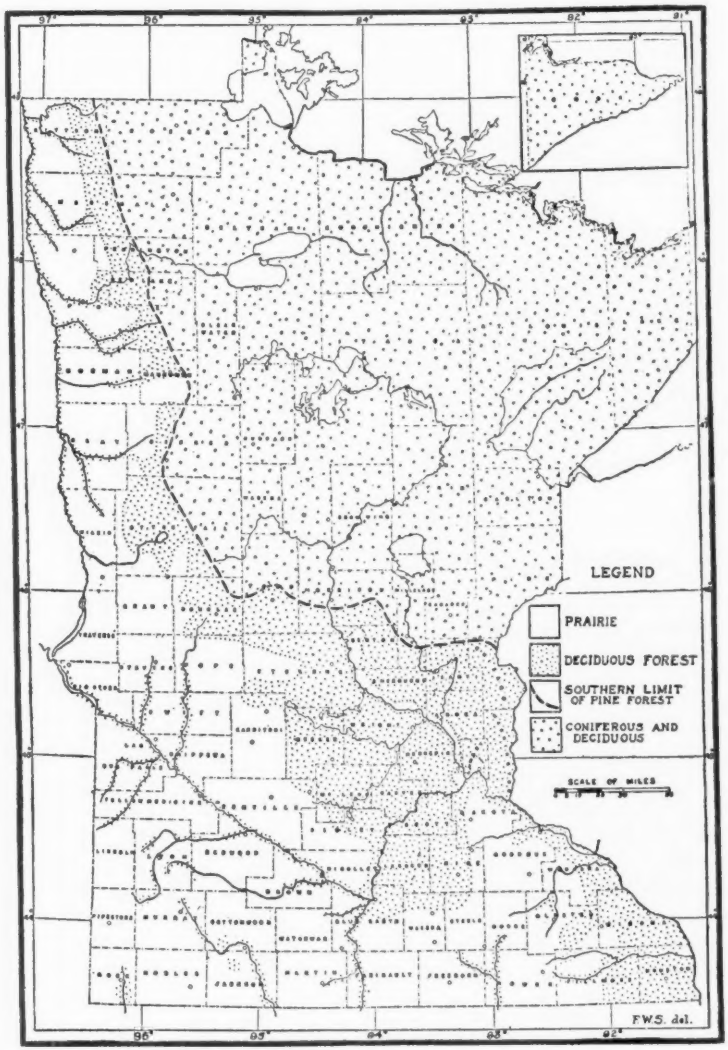

FIG. 1.—Map of Minnesota showing distribution of forest and prairie (after map by WARREN UPHAM and F. K. BUTTERS).

relatively scanty precipitation are typical of grassland climates. Thus evidently the distribution of prairie and forest in Minnesota is determined by the precipitation, not merely because of its small amount, but also by the character of its seasonal distribution. Fig. 2, after PURSELL (**24**), indicates a close correlation between the geographic distribution of the precipitation and the tension line of the prairie and forest.

Comparing figs. 1 and 2, one can readily see that the distribution of broad leaved and coniferous forests in Minnesota is not determined by precipitation, but by some other climatic factor or factors, among which undoubtedly temperature is the most important. The geographic distribution of any plant at its zero point depends upon its ability to reproduce itself. The survival and growth of seedlings and the consequent advance or retrogression of the particular forest type are determined by two main sets of factors: (1) environmental, principally temperature, which is responsible for the early and late killing frost and for determining the length of the growing season; and (2) the hereditary character of the different individuals, which gives special ability to withstand hard environmental conditions.

Most of the conifers, with thick cell sap and various xeromorphic structures, usually withstand a much lower temperature than do most of the broad leaved trees. This would naturally divide the forests of the temperate zones into two great belts: a cold temperate belt, with very cold winters, characterized by the conifers; and a warm temperate belt, with rather mild winters, characterized by the broad leaved trees. The border line between the two belts corresponds to the isothermal line of approximately 43° F. or 6° C. of the normal mean annual temperatures. This line is by no means sharp, however, a broad or narrow belt of transition always being found. The transitional belt between these two great types of forest in Minnesota runs along about the 45th parallel of north latitude, corresponding to the isothermal line of the mean annual temperature of about 42° F., and with the line of an average number of days of the crop growing season about 130 (fig. 3).

EDAPHIC FACTORS.—It is recognized that the distribution of the great plant communities is not governed by edaphic factors.

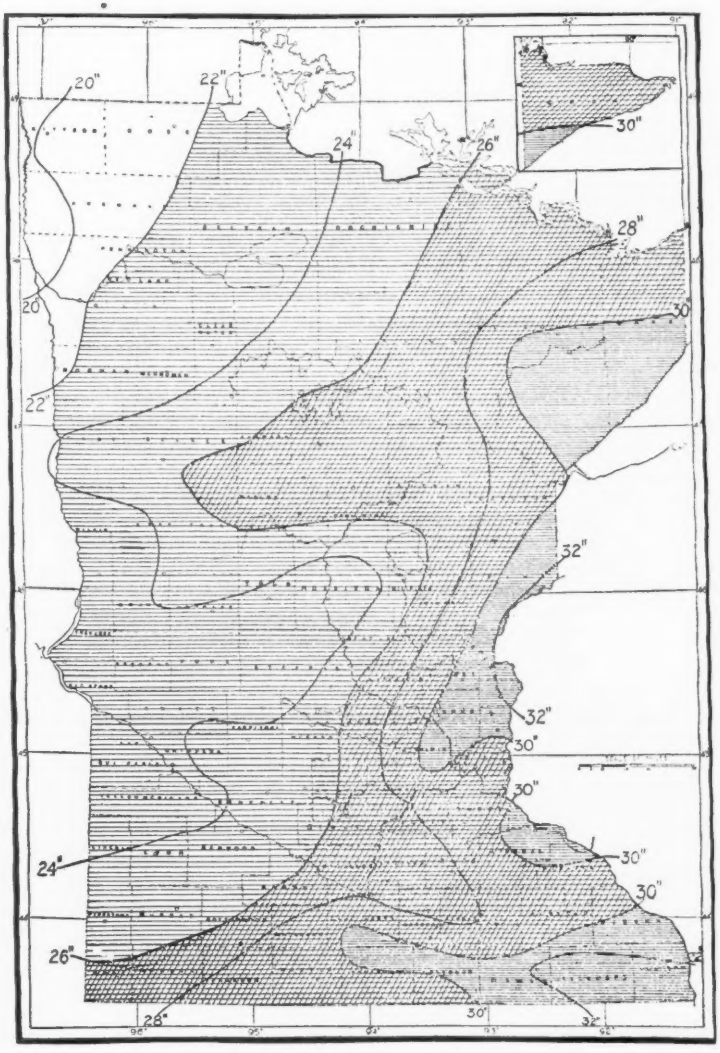

FIG. 2.—Map of Minnesota showing average annual precipitation (after map by U. G. PURSSELL).

This general statement is especially well demonstrated by the distribution of soil and vegetational types in Minnesota. Broadly speaking, there are only three principal divisions of vegetation: west, prairie type; northeast, coniferous forest type; and southeast, hardwood forest type. The soil types, however, are extremely numerous in the different parts of the state. These soils are mostly glacial drifts, and consequently are extremely variable in nature and composition. The Minnesota Geological Survey gives nine principal surface soil formations (fig. 4), each of them containing a variety of soil types. Thus, if we compare fig. 1, showing the distribution of vegetation, with fig. 4, we find such a lack of agreement that we may safely conclude that edaphic factors do not determine the extent of the larger units of vegetation.

Biotic factors.—Among the biotic factors are such plant and animal agencies as affect vegetation. The former comprise parasitic and saprophytic plants, as well as some of the lower forms of vegetation, such as algae, liverworts, mosses, etc. Their effect upon plant succession and the distribution of the larger plant communities is usually very slight. The latter group involves animals, insects, and human influences. The effect of this group on plant succession is usually very marked, and is seen in such changes as are due to grazing, insect invasions, cutting or burning forests, etc., all of which may occur in any place at any time, but are generally confined to rather limited areas. Thus, in the more important changes of a vegetation type these factors are of little significance, although repeated burning along the tension line between two types of vegetation will cause a continuous retrogression in the more advanced successional type. This condition is found in western Minnesota, where the retreat of the forest and the extension of the prairie type eastward are due probably to repeated injury of the forests by fires set by Indians to kill bugs or to convert forest lands into pastures. Although this may not change natural types in the main, constant destruction of forest cover will lower the water table, increase the evaporating power of the air, and bring about more xerophytic conditions, thus shifting the natural border line considerably. In this way it is evident that the distribution of the larger plant communities is controlled by climatic factors,

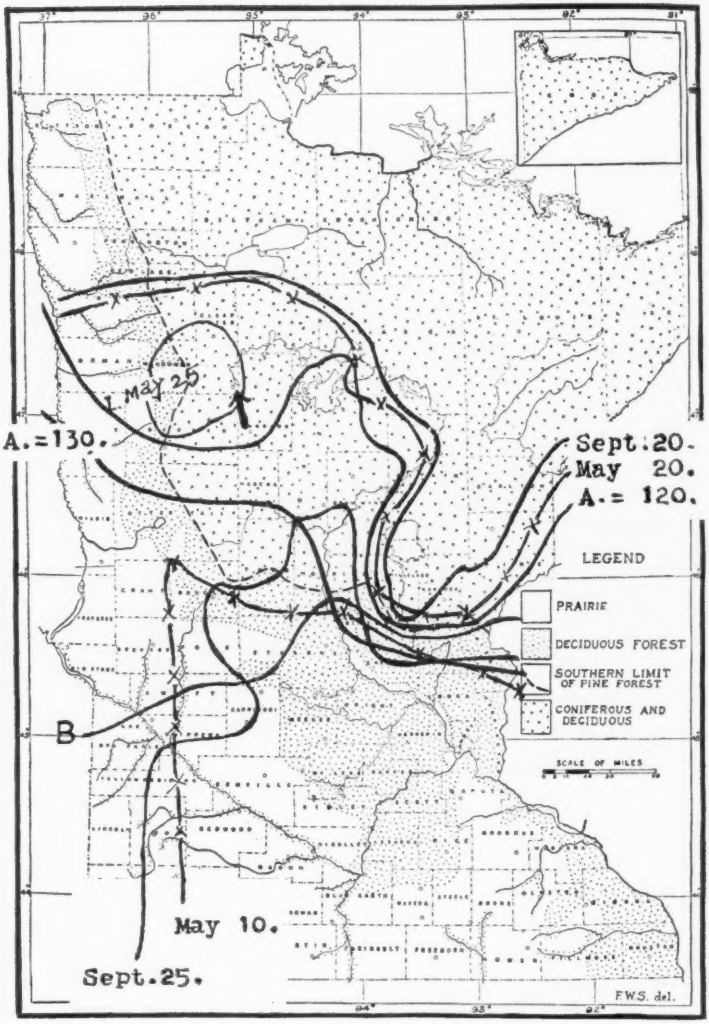

FIG. 3.—Map of Minnesota showing first and last killing frost date: *A*, number of days of average growing season; *B*, mean annual temperature of 42° F.; arrow pointing Lake Itasca.

among which the character and the amount of precipitation determine the extent of the prairie and forest type, and temperature determines the limits of the coniferous and hardwood forest formations. Both the conifers and hardwoods within the transitional belt are supposed to have an equal opportunity in distribution and development, for this belt contains the "zero point" of distribution for both types of forest. The purpose of this study, therefore, is an attempt to discover what factors play the most important rôle in forest successions within the transitional belt.

Study within transitional belt between coniferous and deciduous forest

LOCATION.—Lake Itasca is situated about 25 miles north of Park Rapids, in the southern tip of Clearwater County, Minnesota, 47° N, 95° W. The lake basin comprises an area of about 35 square miles. Lake Itasca is the headwaters of the Mississippi, and hence the basin has been made a state park. At the present time it is probably the only large tract of virgin timber left in Minnesota.

TOPOGRAPHY.—The region is a glacial drift plain dissected by water. The general topographic features therefore are a sandy plain with numerous morainic knolls and ridges dotted by more than a hundred lakes and swampy basins. The highest knoll is 200 feet above the lake surface, and the general relief is about 120 feet (fig. 5).

GEOLOGICAL AND SOIL CONDITIONS.—The entire region is covered by glacial drift. No rock outcrop occurs, but there are large bowlders laid down by the ice. The soils are extremely variable, ranging from those composed of very stony and sandy material to heavy clay with few stones. The soil types are arranged in such a complicated manner that small areas of heavy clay soil are often found within sterile sandy plains, like the general character of glacial drifts in other regions. The glacial deposits also vary with the kind of country over which the ice passed. Thus, in the northeastern part of the state the drifts are composed mostly of volcanic and hard crystalline rocks of the region carried southward, while in the western and southern parts of the state the drifts are mostly of clay with imbedded limestone pebbles. All the calcareous

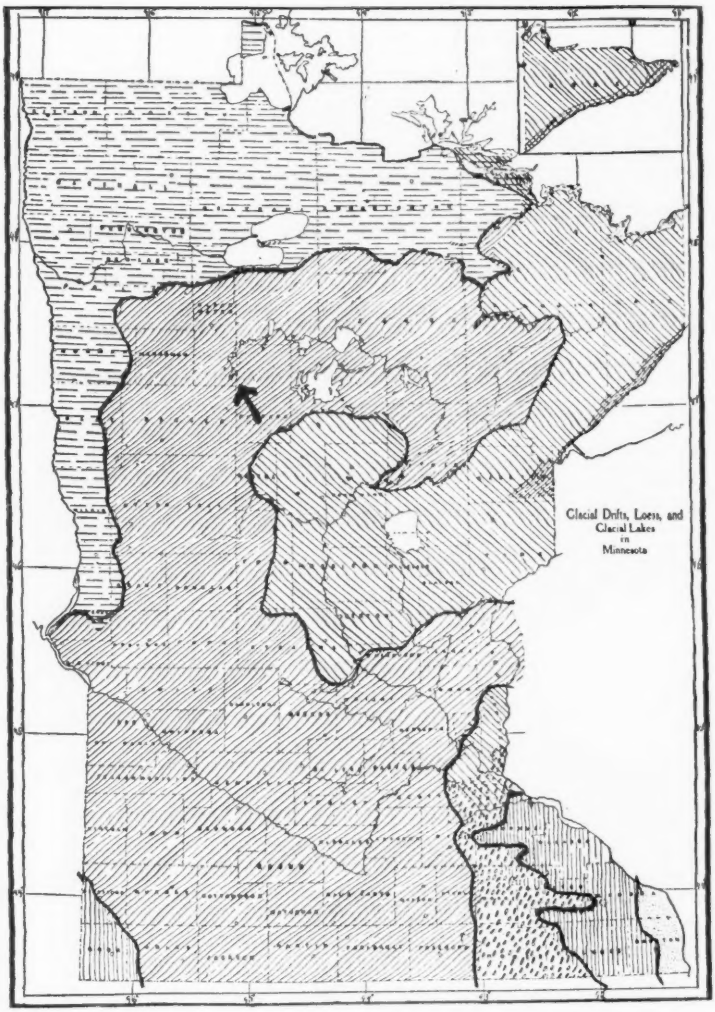

FIG. 4.—Map of Minnesota showing distribution of glacial drifts (after map by Minn. Geological Survey); arrow pointing Lake Itasca.

materials were gathered by the ice as it passed across the shale and limestone country of southern Minnesota, and these deposited in southwestern Minnesota are known as the gray drift. Being situated in a position to receive both types of the drift, Lake Itasca has an unusually large variety of soils.

In places where the soils are rather heavy and able to support a dense growth of vegetation, a layer of organic soil 5 or 6 inches thick has been formed. In places where outwashes occurred, the soil is sterile and unable to support a thrifty growth, and as a consequence very little organic soil has accumulated. Such areas are generally occupied by Jack pines or some other pioneer xerophilous vegetation. The swampy basins and lake shores receive yearly deposits of vegetable matter, hence the humus accumulation on these areas is very thick, and the soil is usually rich and fertile, but generally poorly drained; consequently such areas are usually occupied by black spruce, tamarack, or other xerophilous vegetation.

CLIMATE.—Minnesota has a mid-continental climate characterized by rather warm summers and cold winters. There is no prevailing wind and no high mountain range to chill the clouds and cause local convections, but a large proportion of the low pressure areas which move across the country from west to east touch the state. These areas are preceded by southerly winds and higher temperature and followed by northerly winds and low temperature, and are usually accompanied by cloudy weather and precipitation.

TEMPERATURE.—The average mean annual temperature shown by a continuous record of seven years is 38° F. The average temperature for January is 3° and for July 67° F. The highest temperature is 100° and the lowest −51° F. The average date of the last killing frost is May 25, and that of first killing frost September 15. The number of frostless growing days of the average crop growing season is 110.

PRECIPITATION.—The mean annual precipitation as shown by 25 years' records is 25.66 inches. Probably more than 50 per cent of the total annual rainfall occurs during the summer season, and therefore the winter season is usually dry. Of the mean annual snowfall of Lake Itasca there is no record, but that of Park Rapids is 46.2 inches, which would probably not be far from what we might

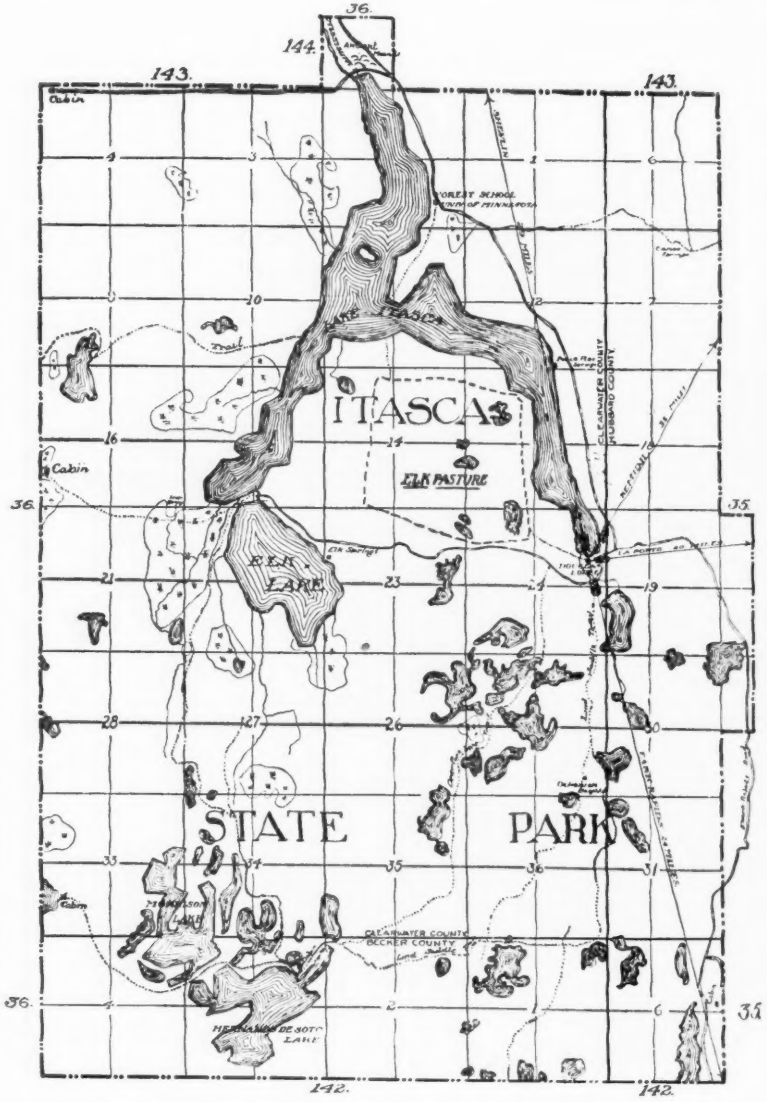

FIG. 5.—Map of Lake Itasca showing distribution of numerous lakes (after map by Minn. Forest Service Bull. 4).

expect at the Lake Itasca region. A rather detailed summation of the climatic components at Lake Itasca for the summer season of 1922 may help in understanding the climatic conditions during the growing season (table I).

TABLE I

Month	Total rainfall (inches)	Maximum temperature	Minimum temperature	Number of days		
				Cloudy	Partly cloudy	Clear
June.....	3.19	94° F.	37° F.	21	6	3
July.....	2.56	92	41	16	8	7
August.....	3.10	101	36	21	5	5

Forest conditions.—Probably two centuries ago the whole region was covered by white and red pine forests, as suggested by the remnants of dead stumps and logs. With the settlement of the region, the virgin forests began to be destroyed This continued until 1891, when the region was made a state park, and some of the virgin pines have thus been preserved. In areas in which the virgin pines were destroyed either by fire or by the ax, a secondary growth of a mixture of jack and red pine together, with a number of deciduous species such as *Betula alba* var. *papyrifera*, *Populus tremuloides*, *Acer saccharum*, *Quercus rubra*, and *Q. macrocarpa*, were developed. The further development of these mixed stands depends upon the kind of soil; hardwoods usually occupy the heavier and more fertile soil, and the conifers the poorer sandy soils.

Among the virgin forests the following associations may be distinguished: (1) pure *Pinus resinosa* type; (2) pure *P. Banksiana* type, which abounds in sterile sandy areas; (3) *Acer–Pinus Strobus* type, which usually occupies fertile and heavy clay soil in limited areas; (4) *Abies-Picea* type, which usually occupies swampy basins or any depression where the moisture supply is abundant; and (5) *Larix* or *Thuja* type, usually found in the swamps or bogs.

Among the second growth five types may be recognized: (1) pure *Pinus Banksiana* type, mostly on sterile sandy soil; (2) pure *Populus tremuloides* type, mostly on very fertile soil; (3) pure *Betula alba*, usually succeeding the aspen stage; (4) hardwood

mixtures, composed of maples, oaks, aspens, birches, elms, and others, which generally occupy very rich soils; and (5) pine-hardwood mixture, composed chiefly of jack pine, red pine, aspen, and birch.

Beside these five types there is also a birch-fir-spruce type, which usually occupies lake shores or any depressions where soil moisture is abundant. On account of the numerous lakes, therefore, this type is predominating the region. In most places where the virgin red pines are standing, this type is developing as an understory. A cross-section of such a forest will show three distinct stories: the

FIG. 6.—Virgin red pine forest at Lake Itasca showing three stories of forest: red pine, birch, and balsam fir-spruce, and showing invasion of balsam fir-spruce reproduction near lake shore.

old pines with open canopy first, the white birch second, and the thicket of balsam fir and spruce third. The age of the virgin trees is 150–200 years, and that of the second growths about 30 (fig. 6).

Forest successions

In studying the forest successions of any region, three periods must be considered, past, present, and future. The last one would naturally lead to a conclusion regarding the climax development of the region. Initial causes are usually classified into primary and secondary series, the former designating that succession which begins from denudation of either bare rock surface, sterile soil surface, or clear water edge, and the latter indicating that successions

may take place in any habitat where the existing vegetation has been disturbed by external factors such as burning, cutting, insect outbreaks, etc. For the natural classification of primary successions COOPER (9) introduced the terms xerarch (for land or xerophytic habitats) and hydrarch (for water or hydrophytic habitats).

PRIMARY SUCCESSIONS

HYDRARCH.—Hydrarch successions in northern Minnesota have been admirably studied by BERGMAN and STALLARD (3). The sequential development of hydrophytic successions from *Chara-Philotria* associes through *Castalia-Nymphaea*, *Scirpus-Zizania*, *Carex*, *Chamaedaphne-Andromeda*, as given by BERGMAN, leading to the *Larix-Picea* associes, is applicable to the situation of this region, but that through *Larix-Picea* and *Abies-Betula* leading to *Pinus* association, which BERGMAN called climax forest, seems hardly to apply to the conditions of the Lake Itasca region. The keynote of a climax forest consists not in the present predominance of a certain species, but in the spontaneous maintenance of its composition throughout future generations. Pines in this region are not only unable to invade *Abies-Betula* associes and reproduce themselves, but are being invaded by the latter (fig. 6). The intolerance of shade by pines compared with *Abies* and the thicket growth of the latter make it impossible for pines to culminate the successions in this particular region.

XERARCH.—The legend of fig. 7 gives a classification of stages of xerarch succession.

Past successions.—The denudation stage.—During the glacial periods this region was covered with ice, probably thousands of feet deep. The pre-glacial flora, therefore, must either have been killed off or swept away by the ice. After the retreat of the ice the region was covered with glacial drifts, upon which the plants started a new succession.

Herbaceous stage.—The initial substratum in this region, unlike many others, was bare soil instead of hard rock surface, and as a consequence the first stage of vegetation would be grasses and herbaceous forms. Among these, bunch grass, sedges, golden rods, etc., may have been present.

Shrub stage.—The availability of soil for a foothold for vegetation would shorten very decidedly the earlier stages of succession. Soon after the development of herbaceous forms xerophytic shrubs such as willows, birches, hazels, and other northern shrubs left behind by glaciers would have come in and driven out the herbaceous forms.

Pioneer forest tree stage.—By the gradually increasing density of shrubby growth the soil surface was shaded and the evaporating power of the air reduced. This resulted in a condition favorable for the germination of some of the pioneer forest tree species, notably *Populus tremuloides*, *Betula alba* var. *papyrifera*, *Pinus Banksiana*, and others that would constitute the first members of the forest succession.

Mixed conifer-hardwood stage.—After the establishment of forest trees the successional development in the region was controlled largely by the kind of soil and the tolerance to shade of different species. At this stage two principal types of soil may be recognized: (1) the sterile sandy areas resulting from glacial outwashes, which were occupied mostly by *Pinus Banksiana;* and (2) sandy loam and clay soils, which are fertile enough to support a dense tree population, upon which a mixture of hardwoods and the three native pines would have been developed.

Segregation of *Pinus resinosa* and the hardwood–*Pinus Strobus* stage.—Owing to the coarseness and looseness in texture and structure of the sterile sandy soils, the organic materials deposited on their surface and the mineral elements set free by physical and chemical agencies in the soil were constantly being leached out by rain water, and the improvement of soil conditions was very slow, and *Pinus Banksiana* continued to occupy this sterile habitat. Meanwhile the struggle for existence among the mixtures on the heavier soils was very keen. The degree of sensitiveness to soil moisture and to the supply of mineral salts and the ability to tolerate shade should mark a step in the succession. Consequently at this stage two types of forests occupying two types of soil would naturally have been segregated: clay soils with higher moisture holding capacity and with a higher percentage of nutritive salts, dominated by the more shade tolerant species such as *Pinus Strobus*, *Acer*

saccharum, *Tilia americana*, *Quercus rubra*, etc.; and the sandy and sandy loam soils with lower moisture and salt content, occupied by less shade tolerant and less moisture and nutrition exacting species, notably *Pinus resinosa*, the timber crop tree of the region.

Present successions.—The principal forest formations of the region at the present time are *Pinus Banksiana* type, *P. resinosa* type, and hardwood-*Pinus Strobus* type.

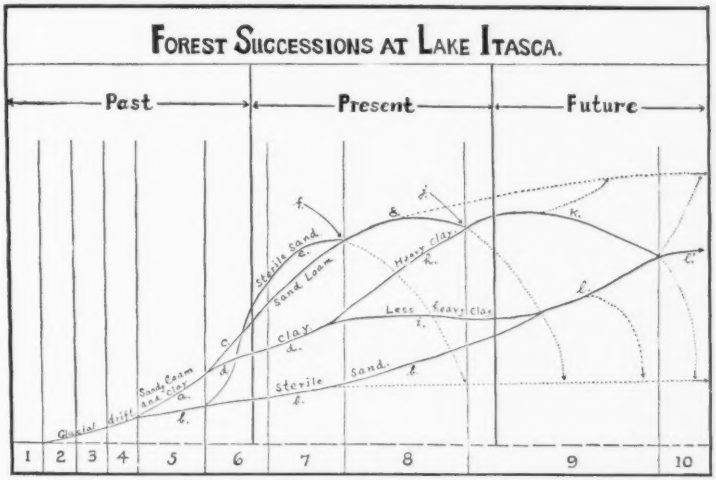

FIG. 7.—Advance of xerarch succession, entire lines indicating courses of primary and dotted lines those of secondary succession: (1) denudation stage; (2) herbaceous stage; (3) shrub stage; (4) pioneer forest tree stage; (5) forest stage (*a*, mixed conifer-hardwood type, *b*, pure jack pine type); (6) segregation of red pine and hardwood-white pine stage (*c*, pure red pine type, *d*, hardwood-white pine type); (7) edaphic climax and transformational stage (*e*, edaphic climax of jack pine type, *f*, transformational mixed jack and red pine type); (8) edaphic climax and parallel development stage (*g*, edaphic climax of red pine type, *h*, parallel development of hardwood-white pine type, *i*, invasion and development of *Abies-Picea* type, *j*, transformational and mixed red pine and hardwood-white pine type); (9) edaphic climax and parallel development stage (*k*, edaphic climax of hardwood-white pine type, *l*, parallel development of *Abies-Picea* type); (10) regional climax stage (*m*, *Abies-Picea canadensis* climax type).

Edaphic climax of *Pinus Banksiana*.—On account of the slow improvement of soil conditions in the sterile sandy soils, *Pinus Banksiana* is free from competition, and hence able permanently to occupy the areas where it became originally established.

Development to *Pinus resinosa* type.—Although most of the sterile sandy soils make imperceptibly slow improvement, some areas, especially those upon which *Pinus Banksiana* had reached its best development, would have been increasing in their organic matter content, and this would result in a decided increase in the moisture holding capacity of the soil, more of the rainfall would be made available, and less leaching would take place. The resultant improvement of the soil would make an invasion by *P. resinosa* both possible and probable. Such an invasion would result at

FIG. 8.—Dying off of *Pinus Banksiana* and transformational stage from *P. Banksiana* to *P. resinosa*.

first in a mixed stand of *P. Banksiana* and *P. resinosa*, and when two species of unequal ecological rank occur together, the inferior or more xerophytic usually gives place to the superior. *P. Banksiana* has a shorter life cycle and is more intolerant to shade than *P. resinosa*, and as a consequence the former is gradually dying out and being replaced by the latter (fig. 8).

Edaphic climax of *Pinus resinosa stage*.—A large percentage of the soils of this region being rather fertile sand and sandy loam, well suited to *P. resinosa* and a gradual increase in the areas of improved sterile sandy soils, conditions are favorable for the regional dominance of *P. resinosa*. This situation is probably present in other

parts of northern Minnesota, and has led BERGMAN and STALLARD (3) to conclude that the climax formation is one of pines. Among the pines they have included *P. resinosa* and *P. Strobus* growing in mixture, and they have further stated that probably the latter would finally replace the former. Conditions of this particular region, however, appeared to the writer such that neither of these two pines would be able to culminate the succession, simply because a true climax forest is not determined by the present quantitative predominance of a certain species, but by the continuity of their reproduction in the habitat which they are occupying. As a matter of fact, both *P. Strobus* and *P. resinosa* not only are failing to reproduce themselves, but are being replaced by either *Acer saccharum*, *Abies balsamea*, or *Picea canadensis* (fig. 6). The present predominance of *P. resinosa* is due simply to the amelioration and the suitability of soil conditions of the present stage, consequently the writer would call it an edaphic climax stage of *Pinus resinosa*.

Simultaneous development of hardwood–*Pinus Strobus* type.—On the limited areas of clay soil at this stage there is a simultaneous development of the hardwood–*P. Strobus* type. Among the hardwoods, *Acer saccharum*, *Tilia americana*, *Ulmus americana*, *Quercus rubra*, *Q. macrocarpa*, *Betula alba* var. *papyrifera*, etc., are the principal tree species. Since these different individuals are growing in a mixture, the competition between them is inevitable. The result of the struggle would again result in the dominance of the superior individual species, the inferior ones remaining in the less suitable habitats. *Acer saccharum* and *Pinus Strobus*, being more tolerant to shade and more exacting in soil fertility, would naturally occupy the heavy clay soils. Owing to greater tolerance of shade and more prolific reproduction, *Acer saccharum* may be able eventually to possess this habitat very completely, forming its climax. *P. Strobus*, on account of its weakness in reproducing itself under too heavy shade, may just fill up openings in the stand. It also seems that the somewhat lighter soils occupied by the other species of hardwood will be occupied, at some future time, by either *Acer saccharum*, *Pinus Strobus*, *Picea canadensis*, or *Abies balsamea*.

Invasion of *Abies-Picea*.—*Abies balsamea* and *Picea canadensis* constitute a large percentage of the forests in Minnesota, being

especially abundant in the northern part of the state, where there are many glacial lakes. In this region, however, no extensive areas of matured forest of these two species are found, but young stands of the two occupy probably more of the surface than do the seedlings of any other tree species, except the pioneer ones such as jack pine, aspen, birch, etc. These latter, as a rule, are abundant everywhere within their ranges. The most striking feature of these two species is that they reproduce themselves readily in any habitat that has room and an adequate moisture supply. Thus the less

FIG. 9.—Mixed type of *Pinus resinosa* and hardwood-*Pinus Strobus*, with prolific reproduction of *Acer saccharum*.

heavy clay habitat occupied by hardwoods and having more open spaces and higher moisture content are more subject to invasion by the *Abies* and *Picea*.

Transformation to *Acer–Pinus Strobus* type.—It has been stated previously that *P. resinosa* cannot culminate the forest succession of this region. The northern limit of *Acer saccharum* extends as far as the Lake of the Woods, more than 50 miles north of this region. Although there are no large areas of matured maple forest, the prolific reproduction of this noted mesophytic climax tree appearing here and there (fig. 9) throughout the region indicates its future development. COOPER (**9**), too, called attention to the fact that

A. saccharum is dominant upon the main ridge at the southern end of Isle Royale, and that southward it is probably able to supersede the conifers and birch. All these indications make it hard to overlook this species as one of the most important competitors for the supremacy in forest succession of this region. Owing to the limited area of suitable soils the present development is slow, however, but the rapid improvement of the sandy loam soils occupied by *P. resinosa*, and the inability of pine to produce itself in its own shade, enable *A. saccharum* to develop fairly rapidly. Fig. 9 indicates the beginning of this transformation. *P. Strobus*, owing to its poor reproduction under dense shade, may hang on with the maple and fill up the openings of the stand, but cannot develop a large pure population.

Future successions.—Edaphic climax of *Acer–Pinus Strobus* stage.—Forests are very susceptible to damage by fire, animals, insects, wind, etc. No matter how well the region is being protected, these accidental injuries can hardly be avoided. Should there be no external disturbance, the constant improvement of soil conditions in the region would enable the *Acer–Pinus Strobus* type to supersede the *P. resinosa* and develop a climax. This climax stage being dependent upon soil conditions, the writer would call it an edaphic climax stage of *Acer–Pinus Strobus*.

Simultaneous development of *Abies-Picea* type.—As stated before, *Abies* and *Picea* reproduce themselves in any habitat that has space and adequate moisture supply. KENETY (**16**), through his intensive studies of *Picea canadensis* in northern Minnesota, concluded that the determining factor for its development is the soil, which has a direct bearing on the moisture supply. This statement shows a marked correspondence with the situation found in this region. Thus a parallel development of *Acer–Pinus Strobus* and *Abies-Picea* type in this region may be expected in future successions.

Abies-Picea climax stage.—Both the development of the mesophytic *Acer–Pinus Strobus* on its optimum soil condition, and the rapid development of the shade enduring *Abies-Picea* type, would lead one to conclude that a parallel development of these two types may culminate the succession, because so far as the tolerance to shade is concerned one type is just as shade enduring as the other,

and soil conditions are probably equally favorable and available for both types. Evidences, however, from quadrat studies on *Abies-Picea* reproduction (fig. 10), indicate that the struggle for supremacy

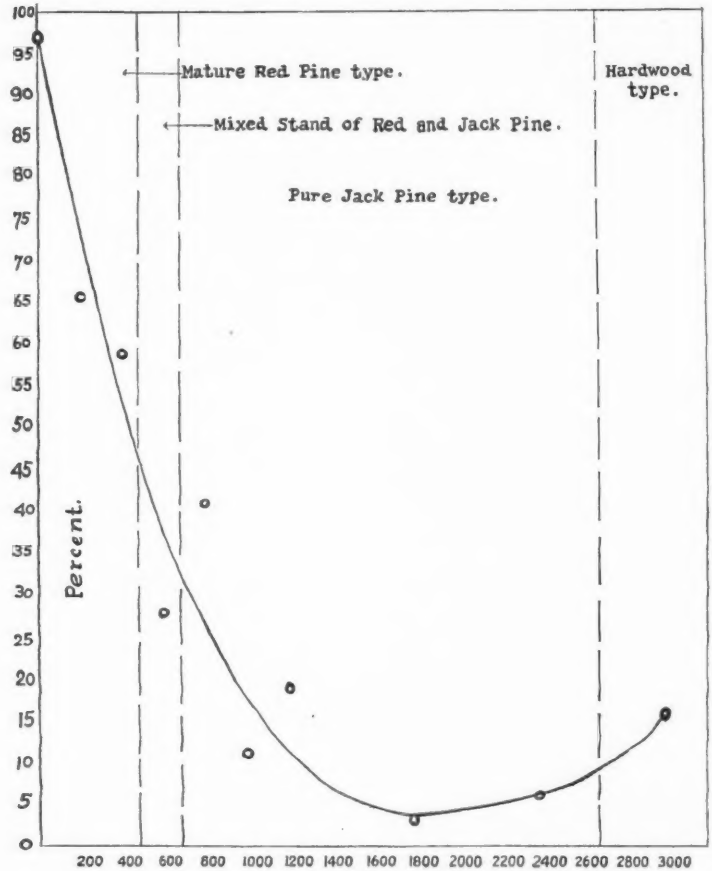

FIG. 10.—Percentage of *Abies-Picea* reproduction from lakeshore inland

in forest succession cannot end in the survival of both of these two types. This parallel development may last for a long time, but eventually the *Abies-Picea* type would probably dominate the climax of the region.

Quadrat studies in *Abies-Picea* reproduction.—The reproduction of the *Abies-Picea* association seems to be best near the margin of the numerous lakes, and less abundant in areas remote from such bodies of water. It seemed, therefore, that the nearness to such water supply as was represented by the lake water determined the relative richness of the reproduction. To test this assumption certain quantitative studies were made. Two parallel straight lines were run by compass at approximately right angles to the western shore of the big lake, for a distance of about one-half a mile. The lines passed through virgin stands of each of the four types of forest characteristic of the region (*Pinus resinosa*, mixed stand of *P. resinosa* and *P. Banksiana*, pure *P. Banksiana*, and the hardwood type). Along these two lines ten quadrats of one-fourth of an acre each (104 feet on each side) on each line were laid out with strings. The intervals between quadrats varied from over 200 feet to over 600 feet, depending upon the distribution of each type of forest crossed. Within the quadrats all the tree seedlings below 15 feet in height were tallied. Taking the total reproduction in each quadrat as 100 per cent, the percentage of *Abies-Picea* reproduction was calculated. The average percentage of the two lines or of the twenty quadrats was plotted as coordinates against the distance in feet away from the lake shore as the abscissae, and an average curve was drawn through the points (fig. 10). This curve shows that the percentage of reproduction of *Abies-Picea* increases in almost inverse proportion to the distance from the lake shore. This indicates that moisture is the determining factor for the development of the *Abies-Picea* type, and the effect of soil is only an indirect one, because even in the sterile sand or jack pine soils, when sufficient available moisture is supplied by the small lakes or depressions nearby, the *Abies-Picea* reproduction is found to be abundant. Since the region is thickly spotted with lakes and depressions (fig. 5), the writer ventures to predict that *Abies-Picea* will probably be able finally to supersede the hardwood-*Pinus* type. A further confirmation of this point may be found in the thicket growing habit of the former, which crowds out the latter very readily. Also other conditions being equal, the lower temperature and the shorter growing season in this region would naturally

favor the development of the northern *Abies-Picea* rather than that of the more southern species.

Secondary successions.—These begin after the destruction of the primary vegetation by external causes, chiefly lumbering and burning. After the removal of the trees, the forest floor is exposed to light. Then the evaporating power of the air is increased, the water table is lowered, and the nutrient constituents may be lost by washing. All these conditions tend to bring about a more xerophytic situation and cause retrogression in forest succession as a consequence. Retrogression, however, depends also upon the degree of destruction and the stage at which the destruction occurred; if a forest is cut with such care as not to cause deterioration of the soil conditions, and at such a stage of a good seedling year as would assure an immediate reproduction of the same species in the habitat, there would be no retrogression in the succession; on the other hand, a reckless cutting may set back the succession for two or three stages.

Burning, unlike the cutting, removes not only the forest stand but all other vegetation as well. As a consequence, in addition to bad conditions brought about by destruction, organic materials are burned up and nitrogen in the soil is liberated, and thus plant succession may be set back to the primary denudation stage. On the other hand, if the fire is not too severe, the burning may be beneficial to forest succession, as light fires usually help to kill back the underbrush, open resinous cones, stimulate germination, and encourage the development of the major forest tree species. The best illustration of such beneficial burning is probably seen in the Douglas fir forest in the Pacific northwest. HOFMANN (14) says, "the principal combination of factors responsible for the preponderance of the Douglas fir formation is the presence of seeds stored in the forest floor, and of fire." When the forest is removed by fire, the stored seeds get conditions favorable for germination and immediately respond to the stimuli. He further concludes that "the Douglas fir formation (*Pseudotsuga-hylium*) is not, as might appear, a retrogression from the cedar-hemlock climax, but is rather a stage of succession preceding the climax."

In general, destructive lumbering and severe fires almost always cause retrogression in forest succession. The dotted lines of fig. 7 indicate where the retrogression of different stages of succession on various habitats may fall. The development of the secondary succession, like that of the primary, depends upon the ability of aggregation, migration, establishment, and competition of the individual species and the differences in initial stages at which the secondary succession commenced. The vegetational cycle of primary successions will then be followed and repeated.

Controlling factors in forest succession

It is obvious that forest successions are controlled, not by a single factor or by a few factors, but by a complex of factors, hence a detailed treatment of all the possible factors, together with some instrumental evidence secured from this region, should be presented. Among the complex of factors, three main divisions are commonly recognized.

Climatic factors

The climatic set comprises all such atmospheric components as humidity, precipitation, temperature, which may be termed direct factors. The evaporating power of the air, which is a summation of all the climatic components which influence the atmospheric control of the water supply, may be termed an indirect factor. The direct climatic factors usually influence the forest successions uniformly over a widespread region. The plant succession that takes place in response to the widespread climatic influence, Cowles (10) has defined as regional succession. This involves long periods of time, and through the operation of climatic agencies may be expressed in terms of eons. Because of the widespread uniformity of climatic factors and the relative permanency of their duration, it seems, according to Nichols (21), that much more is to be gained than lost by ignoring some of the climatic agencies and directing attention to the nearer physiographic and biotic factors, whose operation may occur within periods of centuries and decades respectively (10). Nichols (22) also points out that "in applying the law of the minimum to problems in local physiographic ecology,

climatic factors need not be taken into account, since they are essentially constant throughout the region."

EVAPORATING POWER OF AIR.—Owing to the great variation in vegetation and the lack of adequate instruments devised for measuring even the approximate amount of water lost by transpiration, and lack of means of measuring the amount of water lost through runoff and by percolation, it seems impossible at present to attack the problem of plant growth in relation to the amount of the precipitation of the region. LIVINGSTON (19) tried to solve this difficult problem by devising the atmometer cups to measure the evaporating power of the air, which is the summation of all the atmospheric factors that determine and limit the water loss by plants. The researches of LIVINGSTON (19), FULLER (13), THONE (29), and others have shown some satisfactory results from the use of the atmometer. According to FULLER, the differences in evaporating power of the air alone would be sufficient to account for certain advances in successions. Thus the evaporating power of the air in different types of forest would help to explain the forest successions in this region.

Livingston spherical atmometer cups equipped with the rain-proofing valves as devised by LIVINGSTON and THONE (20) were employed. The reservoir bottles were sunken partly into the ground, so that the cups were about 8 inches above the surface, with one exception, which was hung on a drooping branch about 6 feet from the ground, for measuring the conditions above the undergrowth. Eight stations were established in seven different forest types scattered over the region. Six stations were visited once every five days, and two irregularly. All the readings, except those of the two stations that were taken irregularly, after correction, were plotted (fig. 11). The average daily evaporation rates of the different types for the whole period was reduced, and these, together with mean daily precipitation in cubic centimeters of the period, are shown in fig. 12.

Figs. 11 and 12 show a decided contrast in the evaporating power of the air in different types of forest. The open field, owing to free air movement, higher wind velocity, and stronger insolation, naturally has the highest rate. The cutover land, with scattered

shrubs and primary forest trees, and a resultant checking of air movement and wind velocity, has an evaporation rate second to the

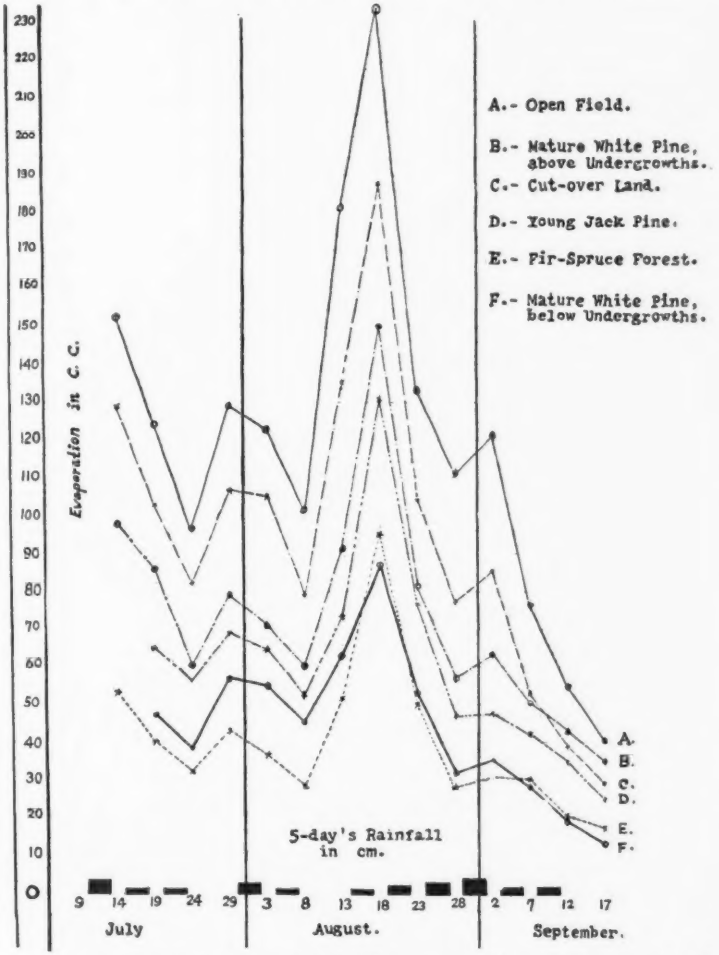

FIG. 11.—Evaporating power of air in different types of forest in 5-day period, and amount of rainfall of equivalent length of time.

open field. In the matured red pine forest, owing to open canopy and lighter soils supporting only a limited undergrowth, the rate is

ranked fourth. The records of the matured jack pine type, owing to disturbances by animals during the course of the investigation, cannot be presented. Judging from a few days' complete record, however, it would be ranked third in the series. In the young jack pine type, owing to its thicket habit of growth, the rate of evaporation is ranked fifth. According to this investigation, the rate of evaporation has probably less influence on succession during juvenile stages. In the matured white pine type, on account of very

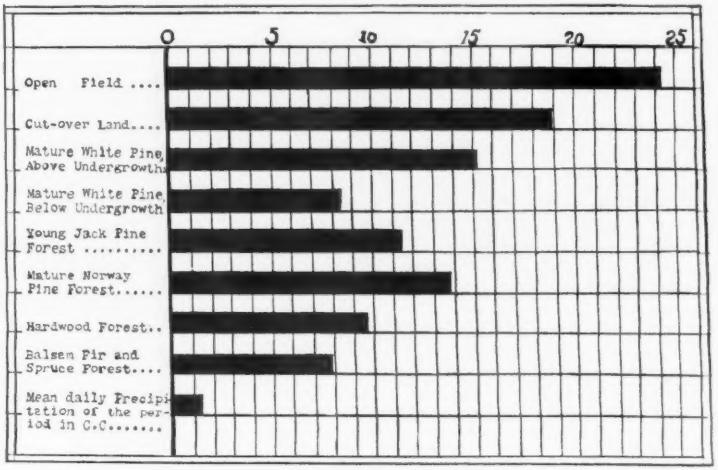

FIG. 12.—Average daily rate of evaporating power of air of different types of forest

dense undergrowth, two stations (one below and the other above the undergrowth) were established. The rate of evaporation at the station above the undergrowth is ranked third, and that of the station below the undergrowth sixth. The hardwood type, with high mesophytic conditions, is ranked seventh, and the *Abies-Picea* type, with its dense shade, is seen to be the most mesophytic of all the types.

These instrumental data show a marked correspondence with and give a greater emphasis to the sequence of forest succession as previously given. Thus, assuming that all the other factors are equal, the differences in the rate of evaporation would tend to cause a sequence

of succession as outlined. Nevertheless, the records of the evaporating power of the air in the lowest stratum of the various forest types for one season is far from sufficient evidence upon which to base any conclusion. The data of FULLER (13) and WEAVER (31) from records extending over three consecutive years, however, prove that while the records in a series of associations varied somewhat from year to year, the same general proportionate relationship was maintained between various associations, and the sequence in mesophytism between the various forest types remained the same throughout the entire period. This unchanging order between the different types in their rate of evaporation is sufficient to justify the belief that one season's records is substantially indicative of the permanent relationship of the communities, and that records extending over many years would result in no essential differences.

EDAPHIC FACTORS

This set of factors includes all those conditions of the substratum that either directly or indirectly influence the growth and development of vegetation. The former comprises soil composition and soil nutrients, soil acidity and alkalinity, soil temperature, soil moisture content, depth and texture of soil. The latter involves surface cover and topography and slope.

DIRECT FACTORS.—*Soil composition and nutrients.*—Broadly speaking, the soil is composed of two general classes of material, minerals and organic matter. The former may be subdivided into two groups; mineralogical constituents (chiefly quartz, which makes up the bulk of the soil), and the nutrient productive particles (such as compounds of aluminum, calcium, magnesium, potassium, sodium, sulphur, iron). All these three kinds of soil particles are found in practically every kind of soil. The solubility and presence or absence of certain mineral elements determine the chemical properties of the soil, and that of the organic materials has more to do with the physical and biological phases. Their relative proportion and availability determine what is generally called the soil fertility. In speaking of soil fertility all three phases must be taken into consideration. The soils of this region have not been studied intensively by any soil specialist. LEVERETT (18) gives only general

information about the surface formation, and ALWAY (1) gives a good account of Minnesota glacial soil studies, but no detailed information for this particular region. The soils are here so intricate as to require a detailed study; therefore no attempt at chemical analysis will be made in this paper, but some of the peculiar characters of the soils that usually support special types of vegetation may be mentioned. The most striking characters are those due to the presence of rich iron compounds and calcareous elements. The former are especially abundant in coarse sterile sand, and more prominent at a depth of 2 feet or more. This may be due to the fact that at greater depths the soil becomes coarse, and the coarser particles are usually chemically inert; consequently more insoluble iron compounds are deposited. RUSSELL (26) calls attention to the fact that soils containing ferrous compounds are generally infertile. This may explain the lack of fertility in the reddish sterile sand here occupied by jack pine. The calcareous materials, on the other hand, decidedly influence soil conditions. Directly they furnish plant food, and indirectly they change the physical condition so as to increase the soil tenacity and soil moisture-holding capacity. The latter is especially important in this region of moderately low precipitation, and has a direct bearing on forest succession. Thus the relative proportion of calcareous materials seems to determine the forest types; the sandy loam soils with less calcareous material being generally occupied by red pine, and the clay soils with a higher calcium content by hardwoods and white pine type. FERNOW (12) and HOWE (15) call attention to the fact that the composition and distribution of forests vary mainly according to the differences in the soils. Fig. 13 shows the sensitiveness of forest types in response to soil conditions. The boundary line of the two forest types agrees so closely with that of the two soil types that the former look like an artificial plantation. The texture, structure, and composition of the soil thus play an important rôle in the forest succession in this region.

Soil acidity.—It is a widely accepted fact that different kinds of vegetation have differences of acid tolerance. The correlation between the hydrogen-ion concentration of the soil and the degree of acid tolerance of the plants determines to a considerable extent

the distribution of the vegetation, and consequently modifies the plant succession. Certain plants, such as species of *Sphagnum*, *Osmunda*, and *Vaccinium*, are usually referred to acid soils, and others, like *Amaranthus*, *Tamarix*, *Chenopodium*, and *Atriplex*, are usually found in more or less alkaline soils. On account of the supposed limitation of such plants to acid or alkaline soils, ecologists have often taken them as indicators of soil conditions. This concept of soil indicators must not be too rigidly held, because more recent investigations show that inferences drawn from the

FIG. 13.—Calcareous substratum underlying coarse sand soil supporting *Pinus resinosa* type on left, and same soil without calcareous substratum supporting *P. Banksiana* type on right.

presence of such supposed indicators are not always correct. *Pinus Banksiana*, *Arctostaphylos Uva-ursi*, *Gaultheria procumbens*, and *Maianthemum canadense* are commonly recognized as acid indicators, but the recent work of KURZ (17) shows that they may be found upon soils with an alkalinity as high as that indicated by P_H 7.5. Thus it is not safe to adhere too rigidly to the idea of acid and alkali plant indicators without taking account of such factors as aeration, soil moisture, and light. KURZ also points out that one must distinguish acid clay, acid sands, and acid peats, which evidently means that the P_H value probably does not account for the

distributional phenomena to such an extent as does the difference in soil types. This statement agrees with the condition of the plant association in this region. In the sterile sandy soils Jack pine is invariably associated with *Arctostaphylos Uva-ursi*, *Vaccinium canadense*, *V. pennsylvanicum*, and *Maianthemum canadense*, while in the loamy and clayey soils occupied by red pine and hardwoods

TABLE II

Soil type	Depth	No. of samples	P_H
	Jack pine		
Sterile sandy soil....	6 inches	3	5.5
	6 inches	5	6.0
	6 inches	2	7.0
	1 foot	10	6.0
	1 foot	8	6.5
	2 feet	3	6.0
	2 feet	3	5.5
	3 feet	4	6.0
	Red pine		
Loamy soil.....	6 inches	2	7.0
	6 inches	6	6.0
	1 foot	12	6.0
	2 feet	4	6.5
	3 feet	4	6.0
	3 feet	1	5.5
	Hardwoods		
Clayey soil.....	6 inches	7	6.5
	6 inches	5	6.0
	6 inches	1	7.5
	1 foot	6	6.0
	1 foot	2	6.5
	2 feet	3	6.0
	2 feet	2	6.5
	3 feet	3	6.0
	3 feet	2	5.5
	3 feet	1	5.0

one can hardly find one of them. This situation would imply that the sterile jack pine soil must be more acid than the others, but the fact is not universally true. About forty soil samples taken from a depth of 6 inches in various soil types of the region were tested by KURZ, and about seventy samples taken from a depth of 1, 2, and 3 feet in various types were tested by the writer with the LaMotte chemical indicators. The results are given in table II.

Table II shows a remarkable uniformity of the P_H values throughout the region. Most of them range from P_H 6.0 to 6.5, with only two exceptions, P_H 5.0 and 7.5 respectively. Also the greater the depth from which the soil samples are taken the more uniform is the hydrogen-ion concentration. Because of these uniform conditions of acidity throughout the region, the writer is inclined to believe that soil acidity has probably no significance in the forest succession. The invariable association of *Pinus Banksiana*, *Vaccinium pennsylvanicum*, and *Arctostaphylos Uva-ursi* seems to the writer to be due not to the acid influence but to the sterile condition of the soil, in which the other plants are unable to grow. Thus, in any habitat that is sterile, competition between the plants is usually not keen, and only the hardy species will survive as a natural association, and they may mislead one into believing that they are acid soil indicators.

Soil temperature.—It is well known that soil temperature does not fluctuate much during the year, and a constant temperature is reached at a depth of 34 feet. The most prominent fluctuation occurs only within the upper 2 or 3 feet. In the forest, owing to dense shade, the fluctuation of soil temperature is much less than that in the open. Nevertheless, it is of great significance to both soil fertility and the development of plant roots; consequently it bears a definite relation to forest succession. WEAVER (31) in his work in Idaho and Washington found a marked relation between the temperature of the soil at various depths and the stage in the succession; he found that the temperature decreases as the climax community is approached. His work (32) at Lincoln, Nebraska, also shows that the soil temperature becomes progressively lower at all depths, from prairie through scrub to forest. The progressive decrease of soil temperature as the climax community approaches is probably due to at least two causes, the increase of shade and the consequent decreased amount of direct insolation, and the increase of soil moisture content as the climax community is approached and the consequent lowering of the soil temperature. The kind of soil should be taken into consideration, of course, sandy soil generally being more readily heated and more rapid in its loss by radiation; while clay both absorbs and loses its heat more slowly, and

has a very uniform temperature in consequence. Furthermore, soil receives heat, not merely from insolation and from the interior of the earth, but also from the decay of organic matter. Rich soils supporting a dense vegetation have more organic matter subject to decay, consequently more heat would be produced by such decomposition. Thus the lower temperature in clay due to higher moisture content may be compensated to a great extent by the products of decay. The soil in this region, as stated before, ranges from bare sand to heavy clay. The records of soil temperature, therefore, followed the natural sequence; that is, the open Jack pine forest with little or no humus cover had a higher average soil temperature than the mesophytic hardwood. It is regretted that, owing to lack of adequate instruments, the soil temperature of various types could not be measured for a considerable length of time; however, a two weeks' record of various types may give a general idea of the sequence (table III).

TABLE III

AVERAGE SOIL TEMPERATURE IN CENTIGRADE OF SEPTEMBER 3–16, 1922 INCLUSIVE

Forest type	6 inches	1 foot	2 feet	3 feet
Pinus Banksiana.....	14.31	14.09	14.16	14.20
Pinus resinosa.....	14.28	14.10	14.14	14.16
Acer saccharum.....	14.10	14.01	14.08	14.09
Abies-Picea.....	13.82	13.78	13.80	13.81

Table III indicates the general sequence of the soil temperature and the different forest types. One should bear in mind, however, that, although the soil temperature is very significant to forest succession, it acts only as an indirect factor, because soil temperature is determined by the kind of soil and the type of forest rather than the reverse. The sterile sand soil, with little or no humus cover, will be frozen earlier in the winter, and, being deficient in shade, will be heated more quickly and dried out more easily in the summer; consequently it will tend to support only pioneer vegetation. On the other hand, the heavy clay soil with slower fluctuations would tend to support a more mesophytic forest.

Soil moisture.—The vital importance of soil moisture to the vegetation has been recognized from the very beginning of ecological

sciences. WARMING (30) classified the distribution of plant communities largely upon moisture conditions. SHREVE'S work (27) shows that soil moisture is the factor that determines the occurrence and distribution of vegetation. PEARSON'S (23) experiments showed that by supplying adequate soil moisture nearly all the species found in the western mountain region are capable of enduring high temperature, and of growing under conditions of lower atmospheric humidity. Thus it becomes evident that soil moisture in relation to plant growth requires critical consideration. Attempts have been made by many workers to establish a definite relation between the moisture supply and plant growth. BRIGGS and SHANTZ (4) first developed the idea of wilting coefficient. ALWAY (1) separated the water into available and non-available by means of the hygroscopic coefficient. CLEMENTS (7) classified soil water into chresard, involving the available, and echard, involving the non-available portion. Since it has been proved that the ability of one plant to secure soil water is little different from that of another, a single valued numerical term to express the soil moisture has been established by BRIGGS and MCLANE (5), known as the "moisture equivalent." On account of adequateness this method was used to secure soil moisture data for studying the forest succession.

The records of all the previous investigations show that the moisture equivalent varies with the different kinds of soil and with the various depths. The general situation is that the moisture equivalent is usually higher on the surface and lower within the subsoil of the same habitat. The critical depth for the development of seedlings probably is not more than 1 foot; therefore, soil samples for this investigation were taken from various depths within a foot of the surface, and from various places within the region, so that a better average for each type of soil as well as each type of forest could be secured. The samples were tested by using a centrifugal force of 1000 times gravity. The average results and the range between the different types of soil and their occupants are given in table IV.

Table IV indicates that the range of moisture equivalent exhibits a distinct correspondence with the sequence of the forest succession, with one exception, the *Abies-Picea* type, which according to the successional series should occupy the soil with the highest

moisture equivalent. As stated before, however, the *Abies-Picea* type is found in any kind of soil that has space and adequate moisture supply. It should be clear, therefore, that a high moisture equivalent does not necessarily mean an adequate moisture supply, nor a low equivalent one that is deficient. For example, the sand has the lowest moisture equivalent of the series, but when it is near to some of the many small lakes or ponds the underground source of supply provides a constant and abundant moisture content. Remote from such open bodies of water, however, it is necessary that the soil possess a considerable water-holding capacity to provide a reserve for the vegetation during the critical dry period of the year.

TABLE IV

Forest type	Soil type	Average moisture equivalent of types
Young Pinus Banksiana	Coarse sand	1.2
Matured Pinus Banksiana	Medium sand	2.6
Matured Pinus Banksiana	Fine sand	8.6
Abies-Picea-Betula	Fine sand	9.1
Pinus resinosa–P. Banksiana	Sand loam	9.9
Pinus resinosa	Sand loam	10.7
Pinus resinosa	Loam	11.2
Mixed hardwood	Loam	14.2
Mixed Pinus resinosa and P. Strobus	Clay	18.3
Acer–Pinus Strobus	Heavy clay	22.4

Thus, aside from the proximity of open bodies of water, the difference in the soil type determining the amount of moisture supply together with the difference in the rate of the evaporating power of the air would determine the forest succession of the region.

Depth and stratification of soil.—In many regions, especially in hilly countries where the soil mantle is usually thin, the relative thickness of soil often becomes a limiting factor in plant succession. In clay country the impervious stratum known as the hardpan is generally present. The poor drainage and bad aeration of such a habitat determine a special type of vegetation. Soils in the region under consideration (except in the bogs and swamps) are remarkably deep, with excellent drainage and aeration, therefore this factor may be disregarded in the discussion of forest successions.

INDIRECT FACTORS.—*Surface cover.*—The surface cover may be divided into two groups, the living cover which includes all the

shrubs, herbs, and grasses, and the non-living cover which includes all organic débris and snow. These two groups have much indirect influence on forest successions.

Living cover.—In these forests nothing perhaps is more striking than the abundance of undergrowth, consisting mainly of *Corylus*

FIG. 14.—Adventitious roots of *Corylus rostrata* within area of 3 feet square

rostrata, *C. americana*, and *Aster macrophyllus*. The first two usually form a dense first story, and the last the second story of the undergrowth. The prolific propagation by means of both seeds and adventitious roots enables them to develop so abundantly that practically no other kind of vegetation is able to grow under them. The soil of the upper 6 inches is practically fully interwoven by their roots and underground stems (figs. 14–16). This thicket growth of underbrush has a tremendous influence on the existence

and development of forest tree seedlings. The competition for space, light, water, and plant food between the tree seedlings and the underbrush becomes very keen. The feeble pine seedlings cannot conquer the dense and thrifty undergrowth. The failure of reproduction in the pines is here largely due to the presence of

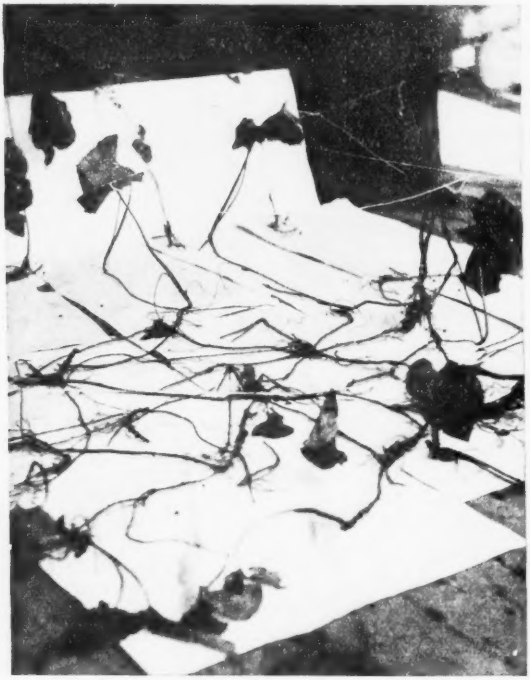

FIG. 15.—Adventitious roots of *Aster macrophyllum* within an area of 3 feet square

this thicket undergrowth. This fact is well indicated by the presence of many one-year old pine seedlings here and there under them, and the entire absence of such seedlings of any greater age. During the spring, which is usually rather dry, the soil moisture in the surface layer (which is generally of duff or humus and not very intimately connected with the subterranean capillary moisture supply) would easily be exhausted by this heavy foliaged under-

growth. Then the dense shade combining with a critical desiccation would be sufficient to kill the feeble pine seedlings.

Non-living cover.—The amount and kind of débris have a decided influence on the radiation and absorption of the insolation, and as a consequence it affects the soil temperature. It also affects the water content of the soil by checking the run-off, increasing the absorption, and lowering the rate of surface evaporation. Here again, the jack pine soil with little or no humus cover has a wider range of soil temperature and a higher evaporation; consequently it is more xerophytic. On the contrary, the hardwood-*Pinus Strobus* forest soils have thick humus cover and are more mesophytic. The duration of snow in different types of forest has also a great influence on the soil temperature and soil moisture condition. In the dense shade of the coniferous forest the snow usually lasts longer, keeps the ground from being frozen, and reduces the loss of water by evaporation; while in open jack pine forest the snow melts more quickly, and the soil is more subject to freezing. All these influences have a share in determining forest succession, but they are of minor importance.

FIG. 16.—Mixed type of *Pinus resinosa* and *P. Strobus*, showing density of undergrowth.

Topography and slope.—Practically all the earlier work in the field of ecology recognized the general effects of topography as one of the most important modifiers of plant succession. COWLES (11) especially emphasizes the importance of topography as a general control over other factors in dynamic plant successions. The dynamic topography or the slopes that are subject to active erosion, strong wind action, and to unequal insolation afford efficient causes for plant succession. In a flat country, however, especially with sandy soil, as in this region, the topography changes slowly and has very little effect on the plant succession.

BIOTIC FACTORS

Among the biotic factors two main groups may be recognized: phytobiotic and zoobiotic. The former includes all influences of plants themselves, and the latter all those of animals and insects.

PHYTOBIOTIC FACTORS.—*Tolerance and light intensity.*—The ability of trees to endure shade is generally called tolerance by the forester. Since light is essential for photosynthesis and assimilation, the relative amount required by each species and the light intensity available become one of the most important factors in forest succession. The tolerance of shade varies not only with different species, but even within the same species, according to the conditions under which the tree is growing. WIESNER (33) states that trees increase their tolerance when they are growing in more fertile soils and under more suitable moisture conditions, and the same individuals would be less tolerant to shade when they grow in precarious conditions. Besides the soil and soil moisture factors, the age, vigor, origin of the tree, and all the climate factors have bearings upon its tolerance. Because so many different factors affect the tolerance of the tree it is extremely difficult to measure the tolerance of a given species, and an exact qualitative value of tolerance of a certain species of tree cannot be found. ZON (34) follows a number of European authorities in proposing a relative scale designating the tolerance of the different tree species. Thus, instead of measuring the amount of light a certain species requires, investigators generally measure the relative

amount of light intensity present in the different types of forest. To measure the light intensity WIESNER first devised an "insolator" and used a sensitive photographic paper. Following the same principle, CLEMENTS (7) invented a "photometer." Recent ecological investigators such as BROWN (6), THONE (29), and others have employed LIVINGSTON'S "radio atmometer" as a means of getting the light intensity through the difference in the evaporation from black and white cups. None of these instruments and means has proved satisfactory. In this study, for the sake of convenience, two thermometers, black and white, were employed. This method, of course, is by no means accurate, but it gives the relative value of the light intensity in different types of forests with a fair degree of accuracy.

The bulbs of ordinary thermometers were wrapped with silk cloth, one with black and the other with white. The two thermometers were then attached to a narrow grooved board. Since we know that black absorbs and white reflects, the difference in readings between the thermometers would be due to the light intensity. The thermometer board was held facing horizontally upward at about 4 feet from the ground, and was carried slowly through the forest along definite lines laid out in such a way that they would cover all the different conditions of the stand. Readings were taken at every 200 feet, and in order to afford sufficient time for the thermometers to adjust themselves to the different light conditions, 10 minutes were allowed for each reading. After each reading the thermometer board was put in a light-proof sack until both instruments indicated the same reading. They were then taken out and the next reading made after the 10 minutes interval. The readings were taken at the same time on the different days. The days for such investigations were of about the same approximate brightness, which was judged by exposing this thermometer board to direct sunlight at the same spot and the same time of the day. The readings thus indicate the difference in brightness. Fifty readings were made in each type of forest. The average results of the different types are shown graphically by fig. 17. The relative light intensity between the different types is expressed quantitatively in table V.

As can be seen from table V, by taking the matured jack pine type as a standard and its ratio as 1, the intensity in the hardwood type is 1/7 and that of the *Abies-Picea* type only 1/10. The weak light intensity in hardwood and *Abies-Picea* type apparently would eliminate the reproduction of pines. The experimental

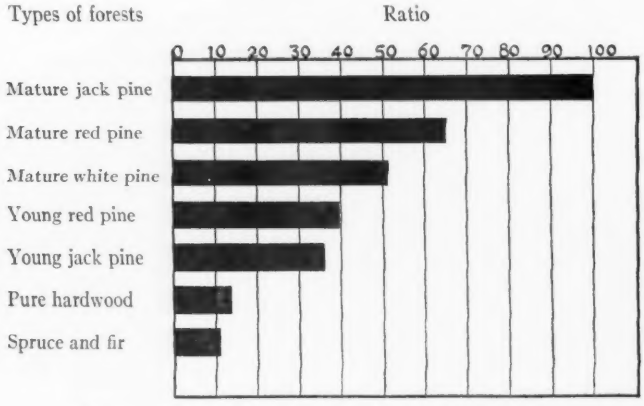

FIG. 17.—Relative light intensity in different types of forest

TABLE V

Forest type	Average difference between thermometer reading	Ratio	Relative intensity in various types
Matured jack pine	1.56	100.0	1.00 (standard)
Matured red pine	1.02	65.3	2/3+
Matured white pine	0.80	51.2	1/2+
Young red pine	0.62	39.8	2/5−
Young jack pine	0.57	36.5	1/3+
Pure hardwood	0.215	13.7	1/7−
Abies-Picea	0.166	9.6	1/10+

records of the Cloquet Forest Experiment Station (**25**) show that the "no shade" plots of *Pinus Strobus* seedlings developed much better than those of "quarter shade," and the "quarter shade" still better than "half shade." For red pine "one-fourth shade" and "no shade" plots were much superior to those of "one-half shade." General observations on pine reproduction in northern Minnesota

indicate the same situation. In open places where seed trees are available one always finds abundant red pine reproduction (fig. 18), while in a dense stand one can hardly find any. BROWN (6) calls attention to the fact that light is one of the limiting factors for plant succession on the Philippine mountains. In this region, although there are many other factors, the ability to tolerate shade and the light intensity under the forest cover should be counted important factors in determining forest succession.

FIG. 18.—Prolific reproduction of *Pinus resinosa* in open near Cloquet, Minnesota

Frequency of seed reproduction.—The frequency of seed reproduction depends upon two main factors, environmental conditions (especially those of soil fertility), and the hereditary character of the different species. Despite the former the difference in the latter may be the limiting factor in determining forest succession. Most of the pines bear seed with definite periodicity. The length of the period is quite irregular, but on the average *Pinus Strobus* has a seed year once in every four, and *Pinus resinosa* once in every seven; while *Pinus Banksiana*, *Abies balsamea*, *Picea canadensis* and a number of hardwoods bear seed almost every year. The infrequency of seed reproduction in *Pinus Strobus* and *P. resinosa* results in a decided advantage to *Acer*, *Abies*, and *Picea canadensis*, and aids them to dominate the succession.

Motility, adaptation, and establishment.—The ability of a species to move out from the parent tree determines its extent of aggregation, and this has a special bearing upon the nature and course of succession. Motility is determined chiefly by the character of the seed and nature of its dissemination: thus seeds of *Populus*, *Acer*, and *Ulmus*, being light and disseminated mostly by the wind, are able to spread much more widely than those of pines. On the other hand, the larger seeds are apt to be carried away by animals to a much greater distance than the lighter seeds are blown by the wind. After the migration of the seeds the ability of different species to adjust themselves to the new habitat determines their establishment. For the adjustment of a plant to new conditions CLEMENTS (8) introduced the term "ecesis," which consists of several processes, germination, growth, competition, reproduction, etc. Here again the three main sets of factors discussed previously have their effect. After all, motility, adaptation, and establishment are important factors to plant succession only during the pioneer stages on areas of denudation, and are of relatively little significance in advanced stages of succession like those existing in this region.

Longevity of trees.—Theoretically speaking, a tree should not die, since a new layer of tissues is always being formed each year. The death of a tree is simply caused by destructive agencies such as fungi, insects, fire, wind, and other unfavorable conditions that reduce the vitality of the tree. The longevity of a tree, therefore, is determined by its ability to resist the destructive agencies and to withstand unfavorable conditions. As a general rule, most of the pioneer species, such as *Populus*, *Betula*, and *Pinus Banksiana*, are very mobile but less resistant to the destructive agencies; consequently they have shorter life cycles than those advanced tree species such as *Pinus resinosa*, *P. Strobus*, and *Acer saccharum*. Those that have the greatest longevity are generally able to dominate the region, but they do not necessarily form the climax of the region, because, as previously stated, the climax of the region is determined not merely by the predominance but by the persistence and continuity of regeneration.

ZOOBIOTIC FACTORS.—These may be divided into two groups, human influences, which consist of cutting, silvicultural treatment,

etc., and the animals and insects. Some of these factors are beneficial and some detrimental to forest succession.

Human influences.—Cutting and silvicultural treatment may bring about progressive succession, or may cause retrogression, depending upon the region and the method of cutting and treatment. In the Adirondack Mountain region, where the virgin forests are mostly mixtures of conifers and hardwoods, the lumberman usually takes out the conifers and leaves the hardwoods. Cutting like this generally advances a stage of succession, because soon after the removal of the conifers the maple reproduction takes place and develops its climax much quicker than would otherwise happen. On the other hand, silvicultural treatment usually takes out the inferior species, such as maple and birch, and makes more room for the pines. Treatment like this generally brings about a mechanical retrogression. Cutting in the region under discussion has been stopped since the creation of the park, and silvicultural treatment has not yet been practiced. Thus for the time being these factors may be disregarded.

Animals and insects.—The effects of animals and insects on forest succession, like those of human influences, may be such as to cause progressive succession or retrogression, depending upon the region and the degree of the influence. In the west overgrazing usually causes retrogression. In the southern pine region grazing generally helps to keep down the undergrowth and encourage the development of the pines, which are generally the climax trees of the region. In the northern woods, during the winter when the ground is covered by snow, deer, rabbits, etc., usually feed on the coniferous seedlings that are covered by the snow. In a region like Itasca, which is under game preservation, these animals are abundant enough to play a part in the limiting factors of forest succession. Insects also may influence forest succession. Among the important insects the spruce budworm may be cited. It has been reported that the last outbreak of this insect was 1910–1919, within which period practically all the spruce and balsam fir within an area of more than 1000 miles from Quebec eastward to the Atlantic were killed back, and birches were left as the dominant tree of the region. A destruction like this would modify forest succession.

In this region, however, neither grazing nor such insect outbreaks seem to have been sufficient to affect succession.

Conclusion

The distribution of the larger plant communities is controlled by climatic factors. The demarkation between the climatic types is by no means sharp, transitional belts of varying widths usually being present. The forest successions within this transitional belt are not controlled by a single factor or by any one of the three sets of factors, but by a complex of factors. In this factor complex the edaphic element, especially the soil composition and soil moisture content, combining with the differences of the evaporating power of the air in different types of forest (figs. 11–13) are the limiting ones in forest succession. The biotic factors, especially tolerance to shade, relative light intensity within each type of forest, and thicket growth of undershrubs which enter into serious competition with tree seedlings for all the necessities of life (figs. 14–16), also play a most important rôle in forest succession. The climatic factors, with the exception of their indirect action through the evaporating power of the air, have very little bearing on the local successions.

Owing to the presence of diversified soil types, a series of edaphic climax types has been, is being, and will be developed. Of these the *Pinus Banksiana* on the sterile sand soils, the *Pinus resinosa* on the sand loam, and the hardwood–*Pinus Strobus* forest on the calcareous clay are the usual types, ameliorated and advanced simply by soil conditions of the region. As time goes on soil conditions are improving, and this would enable a progressive succession to take place or a transformation from one edaphic climax to another. The failure of *Pinus resinosa* and *Pinus Strobus* to regenerate under their own shade, together with the unfavorable conditions of the presence of the thick undergrowth indicates the impossibility of the pines culminating the forest succession of the region. On the other hand, *Acer saccharum* is able to reproduce itself, but is limited to heavy soils. The slowness in the improvement of the sterile sand soils and the limited area of heavy soils in the region make it difficult for *Acer saccharum* to become a climax over the entire area; however, it may develop an edaphic climax and

last longer. The great shade tolerance of the *Abies-Picea* type, with its prolific reproduction on any kind of soil that has adequate soil moisture, as indicated by quadrant study, make it one of the forests best suited to the region. Also, the good water supply, due to the presence of numerous small lakes, favors it to such an extent that it seems both possible and probable that it may develop into the true climax of the region.

Grateful acknowledgment is due to Professors HENRY C. COWLES and GEO. D. FULLER, under whose suggestion and direction the investigation has been conducted. Thanks are due to Professor GEO. D. FULLER for reading this manuscript, and to Dr. HERMAN KURZ for helping to test some of the soil samples. The writer also wishes to extend his appreciation and thanks to the Forest School of the University of Minnesota for their accommodation, and to Professors E. G. CHEYNEY, J. P. WENTLING, C. O. ROSENDAHL, S. A. GRAHAM, and others of the University of Minnesota for their invaluable assistance during the progress of the investigation.

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MEDULLARY BUNDLE IN RELATION TO PRIMARY VASCULAR SYSTEM IN CHENOPODIACEAE AND AMARANTHACEAE

CARL L. WILSON

(WITH NINETEEN FIGURES)

The dicotyledonous families Chenopodiaceae and Amaranthaceae are large families of cosmopolitan distribution and somewhat uncertain systematic position. The Chenopodiaceae contain over 70 genera and 550 species; the Amaranthaceae over 40 genera and 450 species. A large number of species, especially of the Chenopodiaceae, are halophytes. These are frequently prominent and occasionally characteristic components of the vegetation of temperate and tropical seashores, of saline soils, of salt marshes, prairies, steppes, and uplands throughout the world. The majority of the Amaranthaceae are tropical and subtropical, but as a whole the two groups seem to be readily adaptable to a wide range of environment. The forms included in these families are nearly all herbaceous, annuals or perennials, only a few woody and treelike forms falling within the group.

The Chenopodiaceae and Amaranthaceae apparently are closely related, having a number of features in common. SOLEREDER (15), in discussing such structures as the simple perforations of the vessels, the pitting in the prosenchyma, etc., as found in Chenopodiaceae, states that there is no decided anatomical character to differentiate them from the Amaranthaceae. HOULBERT (6) likewise places the two families in close proximity. He holds, however, that the Amaranthaceae are more primitive than the Chenopodiaceae, basing his statement upon the nature of the secondary wood. Relationship, moreover, as based upon flower morphology, must be very close. PAX, writing in ENGLER and PRANTL (4), in his discussion of the affinities of the group Centrospermae, indicates the fundamental resemblance of the floral structure in these two families, their floral formulas being practically identical,

and classes them together as one of the four suborders coming from the Phytolaccaceae. A similar opinion is also expressed by Moss (8). SCHINZ, in ENGLER and PRANTL, in discussing the relationships of the Amaranthaceae, holds that the Chenopodiaceae and Amaranthaceae are so closely related that a differentiation between them is nearly impossible, and that the separation into two families is merely one of convenience.

The anatomy of these two families has long been the subject of investigation by numerous writers. The attention which has been centered upon the groups in all probability is due to the peculiar character of the secondary growth. The characteristic appearance of a cross-section of a stem of one of these plants possessing some secondary thickening is caused by the manner in which the cambium functions. This commonly results in the appearance of a mass of xylem, in which is imbedded small scattered groups or "islands" of phloem. The tissue, however, in which the phloem is imbedded, although consisting of cells with thickened and lignified walls, is only in part composed of true xylem. The xylem present is associated with the phloem in such a manner that collateral bundles are formed. The bulk of the lignified tissue surrounding these bundles has been termed conjunctive tissue, which may be either parenchymatous or prosenchymatous in nature. This tissue very commonly becomes lignified shortly after formation by the cambium, thus resembling xylem (fig. 1). This condition is prevalent in all species of these families, with perhaps one or two exceptions, in which there is secondary growth. It is likewise found in the nearly

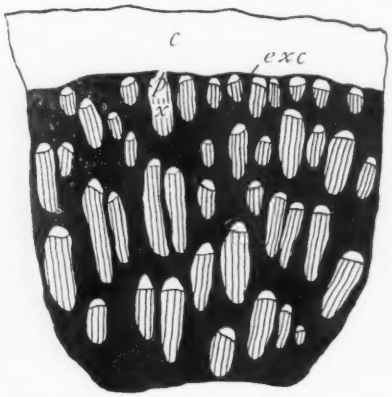


FIG. 1.—Portion of cross-section of stem of *Amaranthus hybridus: c*, cortex; *exc*, position of extrafascicular cambium; *p*, phloem; *x*, xylem; black background represents conjunctive tissue.

related families Nyctaginaceae and Phytolaccaceae. Quite universally distributed in the former family, it is found in some few genera of the latter. An homologous condition, according to SOLEREDER (16), is likewise found in a number of other dicot families and subfamilies, to the number of twenty or more, aside from those mentioned.

In addition to this peculiar type of secondary growth, these families possess another anatomical feature at variance with the usual conditions prevailing in the dicot stem. In several genera the primary bundles of the stem are not arranged in a circle at the periphery of the pith, but are found in the medulla of the stem, separated by several or many cells, of primary origin, from the secondary tissue (fig. 19). In this figure the innermost of the concentric lines represents the position of the extrafascicular cambium, which incloses within it the pith containing the imbedded vascular bundles.

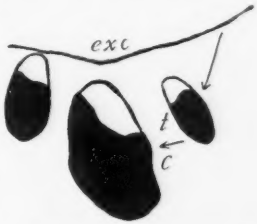


FIG. 2.—*Chenopodium album:* small leaf trace bundle (*t*), after leaving position just under extrafascicular cambium (*exc*), and before fusing with cauline bundle (*c*); both bundles entirely surrounded by primary tissue; direction of movement shown by arrows.

From the time of LINK (7), who was probably the first to publish upon the anomalous secondary growth in these families, research has been directed almost exclusively upon the problems connected with cambial activity and increase in diameter of the stem. These problems deal with such phases of the subject as the relation of the cambium to the primary bundles, and the method of formation and place of origin of the cambium in various species and genera. In general, it may be said that after the formation of the primary bundles, in which (in some forms) a normal cambium may function for some time, a cambium arises in the pericycle. This structure may function in one of two ways: it may continue to produce new tissue during the life of the stem, or it may be replaced successively by the members of a series of concentric cambial rings, each arising, like the first formed cambial layer, in the pericycle. Whether the cambium is permanent or constantly renewed, it

forms, by means of divisions in a centripetal direction, small groups of xylem at intervals, and between these bundlelike groups, interfascicular tissue, the so-called conjunctive tissue. After the formation of a limited amount of xylem, the cambium forms, on its outer face, a small number of phloem cells outside each group. In the meantime the production of interfascicular tissue on each side continues without interruption. According to ARTSCHWAGER (1) and other workers in this field, the cambium cells within the bundle then cease to function, and a new cambial arc arises in the parenchyma outside the bundle, which becomes connected laterally to the interfascicular cambium. It has also been held that the cambium may be unipolar, that is, producing alternately xylem and phloem in restricted areas, the divisions being entirely in a centripetal direction.

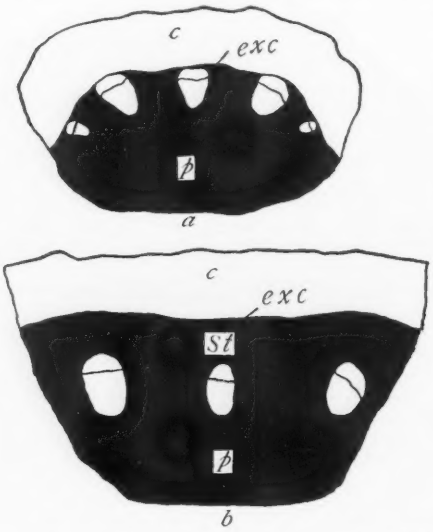


FIG. 3.—Diagram showing apparently medullary bundles: *a*, portion of cross-section of young stem, showing position of extrafascicular cambium (*exc*), in relation to primary bundles, before cambial activity has begun; *c*, cortex; *p*, pith; *b*, position of bundles after some secondary growth; secondary tissue (*st*) cannot be distinguished from cells of pith, and bundles are seemingly entirely imbedded in primary tissue.

Little work, then, has been done upon the primary growth, with the purpose of acquiring a clear idea of the primary vascular system. The only paper of importance dealing with this phase of the subject is that by FRON (5), who presented diagrams illustrating the primary vascular system in a number of species representing various genera of the Chenopodiaceae. In order that the relationship between the primary vascular tissues and the medul-

lary bundles in these families may be appreciated and understood thoroughly, as well as that a general idea of the primary vascular tissues be gained, the following series of diagrams is presented.

For the purposes set forth in the foregoing, diagrams representing the longitudinal course of bundles in the stem are certainly necessary; transverse sections in such cases are insufficient for a proper understanding of the course of the primary bundles. Figs. 2–11 were prepared from serial sections of the stems in question, and represent the cylinder, made up of a system of bundles, as split down one side and spread out in one plane. In following the course of the bundles, examination should also be made of the transverse sections shown in figs. 12–19. In all the forms both cauline[1] and common bundles are shown.

The longitudinal course of the bundles in *Chenopodium glaucum* is shown in fig. 4. The cauline bundles (*c*) are represented by heavy lines; the common bundles by light lines. The point of entrance into the central cylinder of the three bundles making up the leaf trace is indicated by a curved line (*l*). The lateral bundles of the trace pass down the stem for at least two internodes, and fuse with a cauline bundle, one on either side, at some point in the third internode below. The central bundle of the trace traverses four or five internodes before joining a cauline bundle. The leaves are alternate, with a phyllotaxy of two-fifths, which is quite a common arrangement in these families. The cross-section of the stem taken at a node (fig. 12) represents a stage in the growth of the stem at which the extrafascicular cambium has not yet begun to function. The region where this will later develop is represented by the line around the circle of the primary bundles, and in close contact with them. The cauline bundles appearing in this and in succeeding diagrams of transverse sections are indicated at *c*. Two traces having a position at the upper side and lower right

[1] In the opinion of DE BARY (3), who bases his definitions upon the work of other writers as well as his own, cauline bundles may be considered as bundles found only in the stem. The bundles of the leaf trace may have no direct connection with the cauline bundle, unless, as is frequently the case, they are attached to them laterally. On the other hand, common bundles are structures common to both leaf and stem, forming the bundles of the leaf trace and passing down the stem to fuse with cauline bundles at greater or less distances.

are seen entering the stem in this section, each made up of a large central bundle and two smaller lateral ones. These traces are flanked on either side by cauline bundles, which they join farther down the stem. The other smaller bundles are leaf trace bundles

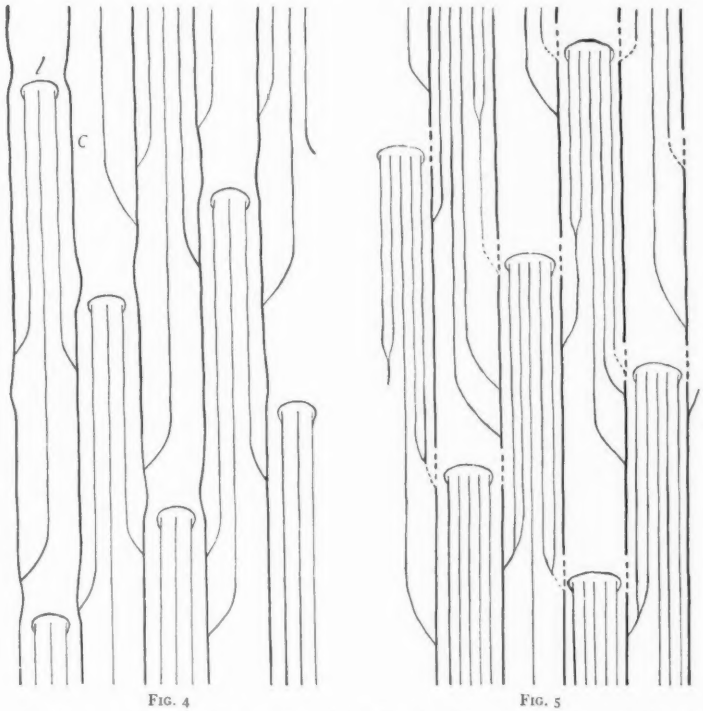


FIG. 4 FIG. 5

FIGS. 4, 5.—Longitudinal course of bundles in *Chenopodium glaucum* (fig. 4), and *C. album* (fig. 5).

which have not yet fused with a cauline bundle in their downward passage in the stem.

Chenopodium album (fig. 5) resembles the first type very closely. The leaf trace is here formed of five bundles, instead of three, which pass down the stem for a distance of from two to four internodes, occasionally anastomosing, before joining the cauline bundles. In this species, as in most of the forms described here, there is more

or less irregularity in the behavior of the leaf trace bundles in their course down the stem, and some attempt has been made to indicate the nature of this irregularity. While the resemblance in the arrangement of the primary bundles to those of *C. glaucum* is close, a rather remarkable departure from the condition in that species exists. The cauline bundle at the node on either side of the entering leaf trace bends inward into the pith for a short distance, and is therefore separated from the first formed cells of secondary tissue by several (generally four or five) rows of primary cells. This condition is represented in fig. 5 by dotted lines, and in fig. 13 by the position of the large cauline bundles (*c*) at the region of the entering leaf trace. In view of the fact that the cauline bundles traverse the pith, for a short distance at least, they may be said to be medullary bundles for a part of their course. The lateral bundles of the leaf trace on one side, sometimes on both sides, descending from above, and joining the cauline bundle at the nodal region, must also become medullary. This follows from the fact that the cauline bundle is medullary in nature at the point where the trace bundle joins it in its downward course, and the bundle of the trace is therefore obliged to leave the peripheral circle of bundles and pass out into the pith for a short distance, in order to reach the cauline bundle and fuse with it (fig. 2).

The two conditions just described apparently are typical of the divisions made by FRON (5) in his discussion of the primary system of the Chenopodiaceae. The first group includes those forms in which the bundles are always an equal distance from the center of the central cylinder; this type FRON terms rectilinear. The second group includes species in which a certain number of the bundles approach nearer the center than other bundles; this arrangement is called undulate. Forms falling within the first group, according to FRON, are not encountered so frequently as those of the second group. In the first class he placed *Salicornia herbacea*, *Haloxylon articulatum*, *Camphorosma monspeliacum*, *Kochia hirsuta*, *Corispermum canescens*, *Suaeda fruticosa*, *Salsola soda*, *Obione portulacoides*, and several species of *Rhagodia*. In the second group, in which the course of the bundles is undulate, he placed *Atriplex*, *Chenopodium*, *Beta*, *Spinacia*, *Blitum*, and *Roubieva*.

The agreement of this classification of "undulate" (the condition just described in *C. album*), a type where the bundle may be medullary for a part of its course, has been confirmed by the writer for a number of species of *Chenopodium* and *Atriplex*. The condition may not be constant throughout a genus, however. For example,

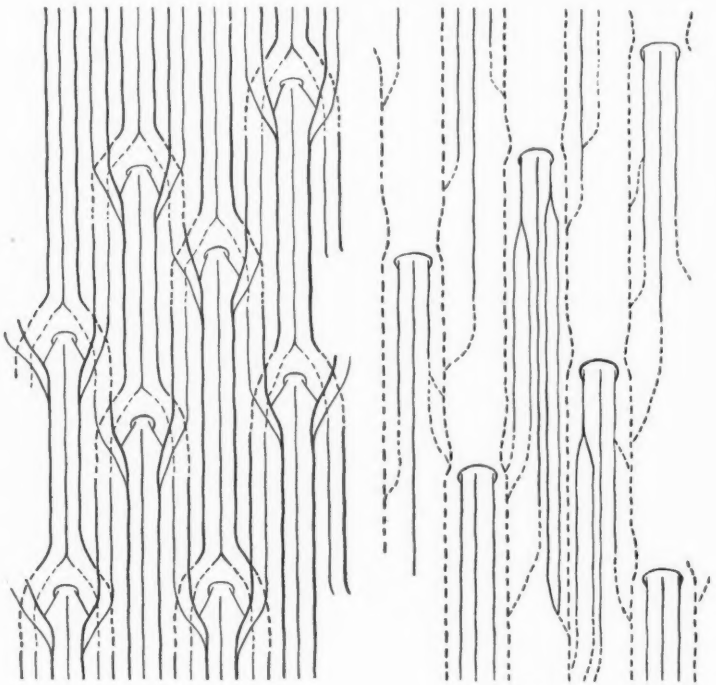


FIG. 6 FIG. 7

FIGS. 6, 7.—Longitudinal course of bundles in *Beta cycla* (fig. 6), and *Chenopodium album* var. *anthelminticum* (fig. 7).

in *C. Botrys* and in *C. rubrum* the cauline bundles pursue a normal course at the node, and this is also true for a nearly related form, *Blitum capitatum*. Moreover, *Spinacia oleracea* examined by the writer has only bundles normal in course.

A drawing copied from FRON, showing the system of bundles in the axis of inflorescence of *Beta cycla*, is shown in fig. 6. The

bundles which are medullary for a part of their course in this form are both cauline and common in nature, as shown by the dotted lines. Again, the bundles of the trace are three in number. The central one splits at a distance of three internodes down the stem from the point of entrance, and the two resulting bundles pass into the pith for a short distance in their downward course (fig. 14). This is a section through a nodal region, and two pairs of bundles having a position in the pith are shown on the right. The outer bundle of each pair is cauline, as indicated. The innermost bundles represent the bundles which have resulted from the splitting of the central bundle of the leaf trace. Each of these leaf trace bundles fuses with the cauline bundle accompanying it two and three internodes farther down the stem. The lateral bundles of the trace to each leaf descend and fuse with a cauline bundle just below the node at which they enter the stem. According to FRON, the course of the bundles is analogous to this form in several other species of the genus, as *Beta martima*, *B. trigyna*, *B. vulgaris*, etc.

In *Chenopodium ambrosioides* var. *anthelminticum* the course of the bundles is very erratic, but the fundamental scheme of arrangement is probably as shown in fig. 7. Of the three bundles to the trace, the lateral ones divide immediately upon leaving the stele, indicating that a possible fusion of bundles may be going on. The central bundle of the trace descends a number of internodes (four or five) before fusion with a cauline bundle, which is entirely medullary in this species. The lateral bundles of the trace likewise descend a number of internodes, as many as three or four, and a considerable amount of fusion and anastomosing takes place before these bundles finally join the cauline bundles on either side. As in *C. album*, the leaf trace bundles likewise become medullary, in this case frequently for some distance, before joining the cauline bundle. In fig. 15, a transverse section of the same stem, the three bundles of one trace are seen at the top of the diagram just after entrance into the stele. Five cauline bundles are shown, all of them separated from the extrafascicular cambium by several rows of cells of primary origin. The remaining bundles consist of bundles of trace which will fuse with cauline bundles farther down.

In Amaranthaceae it will be seen that *Iresine paniculata* presents a very regular arrangement of primary bundles (fig. 8). Fig. 16 represents a cross-section of the stem, taken somewhat below the middle of an internode. The three bundles making up the leaf trace descend in the stem side by side, and fuse with stronger

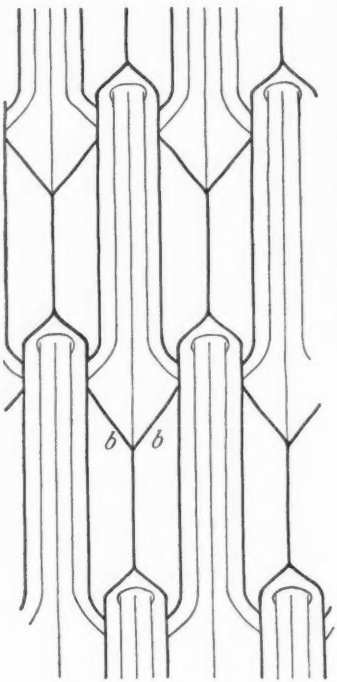


FIG. 8

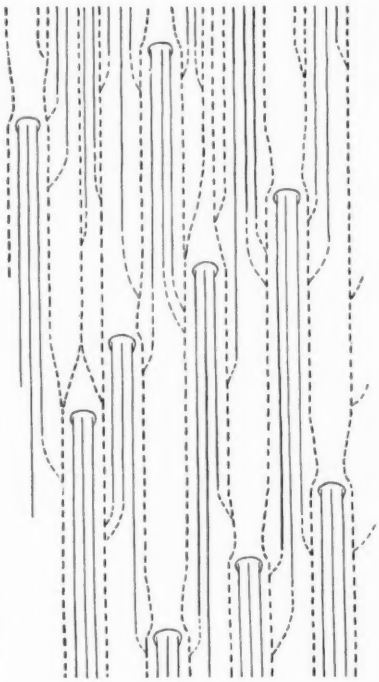


FIG. 9

FIGS. 8, 9.—Longitudinal course of bundles in *Iresine paniculata* (fig. 8), and *Celosia cristata* (fig. 9).

cauline bundles at a point about two internodes from the node at which they enter. In this species large cauline bundles, represented in fig. 16 by the two large opposite cauline bundles, split immediately above the entrance of a leaf trace into the stem, and the two branches descend on either side, thus closing the leaf gap. Descending to the next node, these bundles fuse with the cauline

bundles subtending the leaf trace. The four smaller cauline bundles seen in fig. 16 are the branches resulting from the splitting, above the leaf gap, of the large cauline bundles at the next node above. Branches (*b*) from the bundles subtending the trace form the large cauline bundles, and at the point where these fuse they are joined by the central bundle of the trace descending from above.

The condition in *Celosia cristata*, as shown in figs. 9 and 17, is very similar to that in *Chenopodium ambrosioides*. There are many more primary bundles in the stem, and their course is even more irregular than in this latter species. A cross-section through the nodal region is shown in fig. 17, with a leaf trace made up of bundles irregular in size and shape, shown entering the stele at the top of the diagram. In a section which shows the beginning of secondary growth, the cauline bundles throughout their course are again seen to be separated from the secondary tissue by a few rows of cells of primary origin. The fundamental arrangement of the bundles in this species agrees so closely with that of *C. ambrosioides* that a detailed description is not presented.

In connection with this species, attention should be called to a possible misinterpretation of structure in the stem. The cells of the first formed secondary tissues do not become lignified, either in this case or in a large number of other species in these families. At least the change, if it does occur, does not come about until comparatively late in the life of the stem. These cells become so disposed as to resemble primary tissue. They remain thin-walled, and no distinct radial arrangement is to be observed, the arrangement of the cells being like those of the pith which they adjoin. Later formed tissue becomes lignified and thick-walled, and apparently represents the cells first formed by the cambium. The primary bundles thus appear to be entirely medullary, when in reality they are bordered on the outer side by secondary tissue. In forms like these, therefore, in which the cambium is commonly extrafascicular, the primary bundles appear to be, as DE BARY applies the term, "apparently" medullary (fig. 3). Sections of very young stems prevent any misunderstanding in this respect. This condition, while prevalent in many forms of this group, is

particularly striking in *Celosia*, and attention is therefore called to it at this point.

Several points of difference from preceding forms are shown in *Amaranthus graecizans*, in figs. 10 and 18. In the species last described, it was shown that only certain of the bundles had a position in the pith either entirely or throughout a part of their

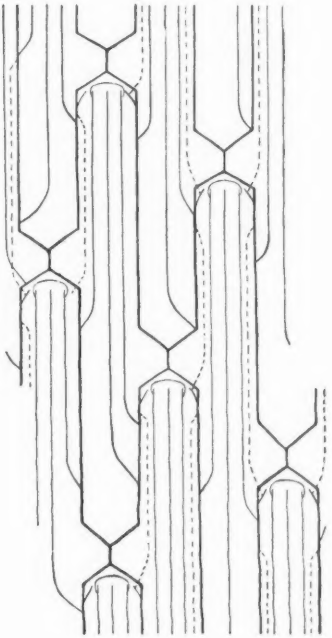


FIG. 10

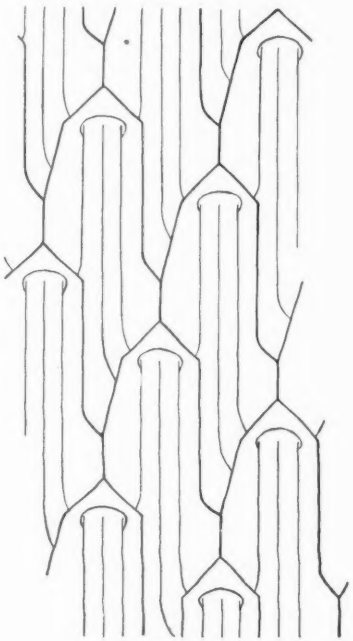


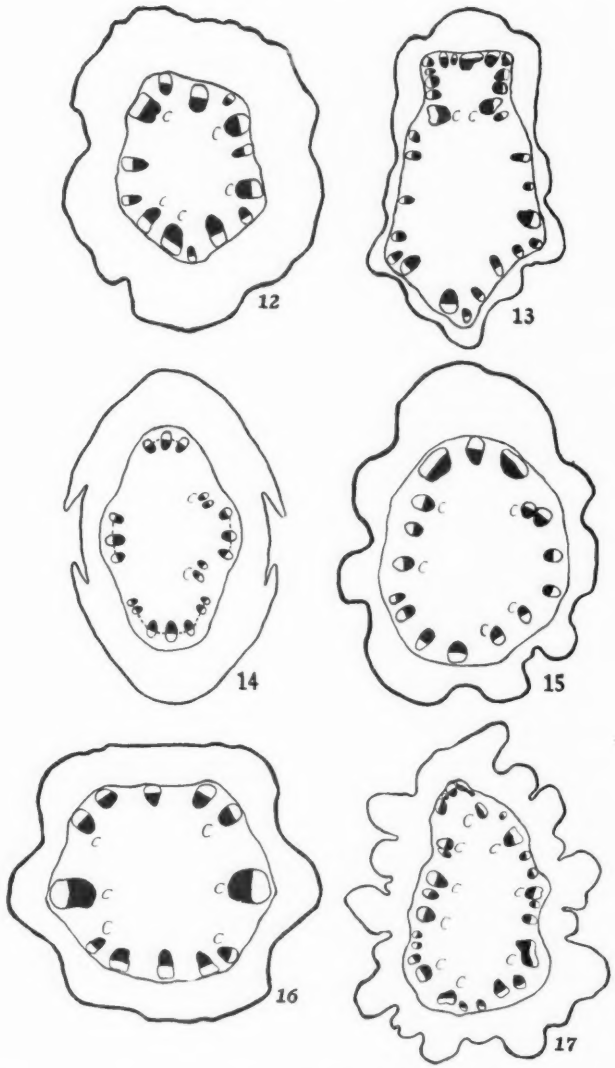
FIG. 11

FIGS. 10, 11.—Fig. 10, longitudinal course of bundles in *Amaranthus graecizans;* fig. 11, *A. hybridus*, showing course of inner circle of bundles represented in fig. 19.

course in the stem. In the form now under discussion, it can be seen (fig. 18) that all of the primary bundles are separated from the region of secondary growth, and imbedded in primary tissue throughout their course in the stem. Another point of difference lies in the fact that the bundles are arranged roughly in two concentric circles. The innermost of these circles is formed by

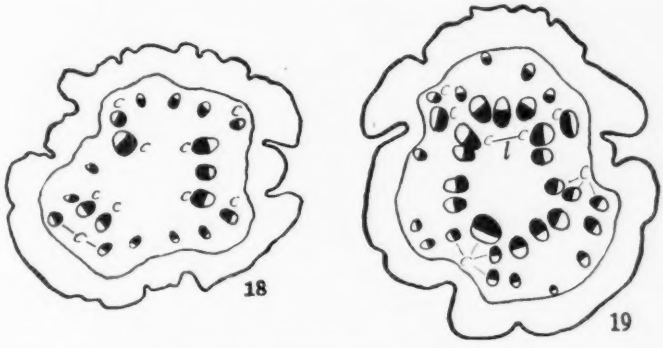
cauline and common bundles, the outer is formed of cauline bundles alone. Fig. 18 represents a cross-section of the stem taken somewhat below the nodal region. At the top three bundles of the trace are seen entering the stem, flanked on either side by cauline bundles. These are properly a part of the inner circle of bundles, but have not yet progressed far enough inward to this position. The cauline bundles of the outer circle are intimately connected with the corresponding bundles of the inner circle. In fig. 10 these cauline bundles of the outer ring are shown by dotted lines. They are seen to take their origin from the large cauline bundles of the inner circle at a region just below the node, pass out of the inner ring and down the stem two or three internodes, finally fusing with a complex of bundles which arises at each node. In most cases this fusion seems to be with a branch trace, just after the trace enters the stem. In effect, the result is a fusion with practically the same elements from which the bundle takes its origin. These outer cauline bundles quite frequently divide once after passing to the outer ring, and on the other hand occasionally fail to appear at all. The small bundles of the inner circle are leaf trace bundles which have not yet fused with the large cauline bundles on either side in their downward course. The leaf gap is closed in the same manner as in *Iresine paniculata*.

In *Amaranthus hybridus* (fig. 19) there are seven, mostly well developed bundles to the leaf trace, as compared with three (occasionally five), as seen in *A. graecizans*. The four outermost of these bundles remain in the outer ring, and together with the outermost cauline bundles make a more definite system of circles. At each node a few bundles leave the peripheral circle of tissue near the entering leaf trace, and pass into the pith, fusing with branches from the large cauline bundles (connected by the line *l* in fig. 19) of the inner ring on either side of the entering trace. The four small outermost bundles of the trace fuse with the group of bundles thus formed, all the bundles ultimately joining the large cauline bundles previously referred to, on each side of the trace. There is thus seen to be a connection between the peripheral circle of bundles and the medullary system of bundles. The course of the bundles is again apparently very irregular, and various conditions



FIGS. 12–17.—Stem cross-sections at nodal region: fig. 12, *Chenopodium glaucum;* fig. 13, *Chenopodium album;* fig. 14, *Beta cycla;* fig. 15, *Chenopodium ambrosioides* var. *anthelminticum;* fig. 16, *Iresine paniculata;* fig. 17, *Celosia cristata.*

prevail. For instance, one of the outermost of the leaf trace bundles may descend the stem several nodes, and then pass into the peripheral circle of bundles, so that the cambium of the bundle is continuous with the extrafascicular cambium. The bundle would thus again connect the medullary system with the peripheral secondary growth. It is unnecessary to discuss such irregularities at length. The fundamental plan of the primary system in these two species appears to be the same, although that of *A. hybridus* is the more complex. This is due to the fact that there are more well defined bundles to the trace, and also that the cauline bundles



FIGS. 18, 19.—Stem cross-sections at nodal region: fig. 18, *Amaranthus graecizans* fig. 19, *A. hybridus*.

of the outer circle always divide into two and sometimes three bundles before proceeding down the stem. The complexity of the stem is such that a diagram showing the course of all the bundles at once would be difficult to interpret. For this and for other reasons to be brought out later, a diagram has been prepared (fig. 11) showing the longitudinal course of the bundles of the inner circle only, as seen in a transverse section of the stem. The diagram is thus made up of cauline bundles and the three innermost bundles of the leaf trace. These latter pass down the stem and fuse with the cauline bundles in the usual manner. The leaf gap is closed in the same manner as in *Iresine* and *A. graecizans*. Based upon the material so far examined, such species as *A. blitoides* agree

with the condition in *A. graecizans*. Other species, such as *A. retroflexus*, *A. gangeticus*, *A. salicifolius*, *A. Torreyi*, and *A. caudatus*, accord with the condition in *A. hybridus*.

Discussion

Medullary bundle

Of all the departures from normal structures in the dicot stem, the medullary bundle is one of the most striking. It occurs in a large number of unrelated families, perhaps thirty or more. The exact number of families in which it is found is difficult to determine, because of the confusion of terms applied by various writers. The term "medullary bundle" is quite commonly applied to intraxylary phloem, better known as internal phloem, which is present in a number of dicot families. In such cases, groups of protoxylem occasionally lie closer to the phloem than to the metaxylem, and hence appear to accompany the former rather than the latter. This further adds to the confusion, since there thus appears to be present a ring of medullary bundles. According to our present conception of internal phloem, however, these detached portions are phylogenetically portions of the vascular ring of bundles.

Weiss (18) and Col (2), who appear to be the chief contributors to the subject of true medullary bundles, in studying these structures in various families, found that medullary bundles are generally common bundles, rarely cauline. They do not ordinarily constitute an independent system in the stem, but are in connection with the peripheral circle of bundles at the node, and are most frequently an evident and direct prolongation of the normally situated bundles.

So far as the writer has been able to find, but little attempt has been made to account for this departure from the normal fundamental type of dicotyledonous stem. Col (2), in attempting to account for the condition in various families with which he worked, found a crowding at the node due to the large number of bundles coming in from the leaf and floral regions. He therefore claimed that since no space was available in the periphery, the bundles were crowded into the pith and cortex. It would seem pertinent to quote Sinnott (14) in this connection:

Against the argument that medullary bundles in ferns are caused by the influence on the stele of the complication of the petiolar bundle, it may be pointed out that in the Marattiaceae the intricate vascular systems of stem and leaf communicate with one another by only a double trace, and that in young plants of *Pteris* a medullary bundle appears in the stele, while the leaf trace is still a very simple strand.

WESTERMAIER (19) mentioned several species of *Begonia* in this connection. These species are perennial by tubers or rhizomes. According to this writer the amount of translocation taking place in such a plant, as compared with woody forms, makes necessary the development of other bundles in the pith to supplement those of the normal ring of bundles. PETERSEN (10), in his discussion of internal phloem in *Campanula*, describes transition stages between internal phloem and medullary bundles. Several forms have internal phloem closely associated with the peripheral ring of bundles or in isolated groups. In another case medullary phloem was found with which xylem was associated. A transition is thus built up to other species with well developed medullary bundles. It is probable that PETERSEN had in mind a phylogenetic development of medullary bundles in this genus, although this is not certain from the context of his paper.

In whatever manner such conditions arose, it is difficult to conceive a situation in which they arose suddenly to the form in which we now observe them. A series of steps, we must believe, has intervened between some generalized form and the present apparently specialized condition. Further, our present conception of the origin of many plant structures leads to the belief that such conditions must have had a long evolutionary history, analogous to the history of other plant structures which have been studied by various workers in recent years. Evidence of a geological nature in support of this may be somewhat lacking, but this does not necessarily invalidate the conception. It has become almost axiomatic that the origin of a species or group is not necessarily indicated by the earliest records of their discovery. ZEILLER (20) states that the earliest fossil remains of herbaceous species of any of these families are fruits of a species of *Salsola* in the Tertiary of Europe. Leaf impressions of various species of *Pisonia*, a genus

of the nearly related family Nyctaginaceae, have been found in various formations of the upper Cretaceous in this country and Europe. *Pisonia*, however, is a woody genus. It would seem, therefore, that so far as geological evidence goes, the Chenopodiaceae and Amaranthaceae may be of somewhat recent origin. As previously stated, however, this evidence should have little weight, and the complexity of the groups as seen in the medullary bundle and type of secondary thickening would suggest much specialization and greater age.

In spite of structural similarities, it is highly probable that the medullary bundle has arisen independently in the various groups in which it is found. This is made all the more probable when one considers the totally unrelated families in which the structure is prominent, as the Piperaceae and the Campanulaceae. This conception is supported by SCOTT and BREBNER (13) in their explanation of the origin of anomalous secondary growth in the Iridaceae. This growth bears a remarkable resemblance to the same type of growth as found in Liliaceae. They say "it is very probable that the first origin of secondary growth may be taking place today, just as we find medullary bundles appearing in certain dicots as an individual peculiarity."

The medullary bundle is not a structure of wide distribution in the two families treated here. The type of bundle arrangement as seen in *Amaranthus* was first noted by LINK (7), and apparently is widely distributed, if not universal, in the genus. Medullary bundles were reported by REGNAULT (12) as occurring in *Chenopodium ambrosioides*. VOLKENS, in ENGLER and PRANTL (4), recorded their presence in *Acroglochin persicarioides*. This last writer states that there are eight cauline bundles in the stem of this plant.

Assuming that such an arrangement of bundles as seen in *Amaranthus* is the highest type in these families, the species of the two families so far studied have been arranged in a manner which seems to be in accord with a possible method of origin of the medullary bundle in these, or in other groups. The view is here advanced that the medullary bundle has arisen by the gradual advance of bundles from the peripheral circle of bundles into the pith. This

change has most probably originated at the node, and gradually extended up and down the stem. The influence of any two successive nodes gradually makes itself felt throughout the internode. It is highly probable, according to the evidence presented here, that the cauline bundles were foremost in this inward progression. This statement is based upon the species just described, such as *Chenopodium album*, *C. ambrosioides*, and *Celosia cristata*, in which the cauline bundles have advanced into the pith, either at the node only, or for the entire length of the bundle. The common bundles remain at the margin of the pith, in connection with the extrafascicular cambium. That this is probably not the usual order of evolution is shown by the fact, already stated, that medullary bundles as a whole are said to be leaf traces.

Chenopodium glaucum and *Iresine paniculata* may be taken as representing a more generalized type of dicot stem. The first departure in the direction of a specialized condition may be found in such a form as *Chenopodium album* (figs 5, 13), in which, at each nodal region, the cauline bundles pass into the pith for a short distance, quickly returning to their peripheral position. The influence of the node, if such it may be termed, becomes more powerful in such a species, as shown in figs. 6 and 14, copied from FRON. Here this influence operates to such an extent that the divided leaf trace bundle on either side of the node is affected equally with the cauline bundle on each side, and both bundles pass into the pith. This is indicated by the dotted lines in fig. 6, and by the two medullary bundles on each side of the entering leaf trace at the right in fig. 14. As in the preceding form, this medullary course of the bundles is of but short duration, and the two bundles in their downward course quickly return to their former position. *Chenopodium ambrosioides* (figs. 7, 15) exhibits the next step in this possible progression, in that the cauline bundles are wholly medullary, although as yet very close to the extrafascicular cambium. The common bundles, however, remain in connection with the extrafascicular cambium for a considerable distance before moving into the pith to join the cauline bundles. This form, however, may be taken to represent a stage near the culmination of this evolved condition, at least in this family.

Turning now for evidence to the Amaranthaceae, *Celosia cristata* is seen to be quite similar as regards the course of the bundles to the form just described. This species, therefore, may be taken to represent a stage at the same level of development in this family which *Chenopodium ambrosioides* represents in the Chenopodiaceae. This suggests that the medullary position of the bundles may have evolved independently in the two families, since homologous stages in development may be found in each family.

Amaranthus is used in this paper to represent the highest point of development of the medullary condition, at least in these two families. This is supported by the fact that all primary vascular bundles are entirely medullary, and the only connection with the tissue at the periphery of the pith takes place at the nodal region. Here again it would seem that the cauline type of bundle has probably been foremost in this inward movement of bundles, since these are found lying deepest in the pith. It is true that branches of these bundles pass into the outer ring of bundles, but this might be held to be due to the influence of the nodal region, where these changes take place.

Some significance may be attached to the diagram shown in fig. 11. Here, as previously described, only the inner circle of bundles seen in fig. 19 is incorporated, no connections to the outer ring of bundles being shown. A fundamental resemblance to the other species can be seen in the manner in which the leaf gap is closed, in the course of the trace bundles, and in the manner in which they join the cauline bundles. In view of these facts, such a species is held to be a derived form, so far as primary anatomy goes.

It is not intended that the idea developed in the foregoing be a conclusive statement as to the method by which the medullary bundle has evolved in all the dicot families possessing that structure. It is a possible method by which this type of structure may have originated and developed in these groups in particular, and possibly in other families. The medullary bundle, then, is a structure occurring in a number of dicotyledonous families, the significance and function of which is unknown. The origin and history of development of such a disposition of bundles are debat-

able, however, and considerable speculation concerning it would be permissible, if for no other reason than that of stimulating further work of a comparative nature in this direction.

Primary vascular system

Some attention should first be given to the taxonomic value of such structures. In order that use may be made of plant structures in deciding affinities, it is evident that there must be available a large body of knowledge in the field. In using such characters as the nature of the primary vascular system to this end, the worker is handicapped by the lack of information available on the subject. Of the small amount of research which has been carried on in this direction, nearly all has been done by the earlier students of plant anatomy. In this connection should be mentioned the pioneer work of Nägeli (**9**), who figured a number of diagrams of primary vascular systems, which have been extensively copied by textbook writers since his day. De Bary (**3**) reviewed the facts as known to him, and since that time but few papers have appeared containing material of this type. Since little is known about the primary anatomy in general of our great families and alliances, it is difficult to evaluate and make use of such evidence from the standpoint of determining relationships.

In the families concerned here, it appears, at least from the comparatively few genera about which information of this kind is available, that the primary anatomy might possibly be significant in this direction. The great majority of investigated species have a bundle system made up of both cauline and common bundles. They thus depart from what has been called the dicotyledonous type, in which all the bundles of the stem are leaf trace bundles. The presence of both types of bundles is not universal, however. The writer has found that in the cases of *Gomphrena globosa* and *Spinacia oleracea* all the bundles of the stem are common bundles. It has already been stated that Fron presented diagrams which illustrated the primary vascular system in a number of species of Chenopodiaceae. Several of these, which represent various genera, possess a leaf trace of but one bundle. This condition is probably due to reduction, as the species in which it occurs are

halophytes. A comparison can be drawn, however, between the species FRON figures, in which no indication of reduction occurs, and the diagrams presented here. The general impression is reached that the arrangement of the primary bundles offers significant evidence as to the close relationship of these families. This conclusion is reached chiefly from the fundamental arrangement of the bundles shown. The chief indications rest upon the relation of the cauline and common bundles. The species figured by FRON which show indications of reduction may be included in this comparison. Fundamentally their arrangement is the same as the other species considered. It is doubtful what emphasis should be placed upon the number of bundles of the trace, as these vary. The number of cauline bundles, too, appears to be variable. It might seem desirable to proceed farther and in greater detail in this comparison, but lack of a wider knowledge of primary systems in these and other families makes the matter difficult. Little or no information is available which would show that a certain type of primary structure is constant throughout a family. From the material presented here, it would seem that a definite arrangement of primary bundles is characteristic of these two families.

The family Dioscoreaceae possesses a type of primary vascular system which merits our attention at this point. First, however, a word should be said with reference to an anomalous type of secondary thickening found not only in this family, but also in a number of genera belonging to several other families of the Liliales. The fact has already been mentioned that this condition is almost exactly paralleled by the peculiar type of cambial activity found in the families treated in this paper. The general appearance of the tissues, and the manner in which they are produced, is fundamentally the same in both groups. Several early writers, including SANIO (**17**), have called attention to this, although so far as the writer is aware there have been no important discussions calling attention to a possible phylogenetic interpretation of this condition. A superficial observer, however, taking these facts, together with the monocot stemlike arrangement of the primary bundles in *Amaranthus*, might speculate upon the relationships of the Amaranthaceae and the Liliales. For this reason it has seemed best to

discuss briefly some of the factors having to do with relationships in these groups.

According to DE BARY, the dicotyledonous type of primary system is characterized chiefly by the fact that the vascular system of the stem is made up only of bundles of the leaf trace. This he says characterizes not only the majority of the dicots, the Coniferae, Gnetaceae, Osmundaceae, and *Equisetum*, but likewise Dioscoreaceae. With the exception of this family, the primary anatomy of the members of the Liliales which possess anomalous secondary growth is of the monocotyledonous type. Later investigations, however, have shown that the Dioscoreaceae do not belong in the class in which they were placed by DE BARY. The researches of QUÉVA (11) have shown that the primary anatomy of the family as a whole is characterized by being made up of both cauline and common bundles. He figures diagrams of the course of the bundles in longitudinal view which, although simpler, closely resemble the diagrams shown in this paper. The node is trilacunar, however, that is, each of the three bundles of the trace causes a gap of its own as it leaves the stele. The Chenopodiaceae and Amaranthaceae are mostly unilacunar, that is, but one gap is left in the stele as the leaf trace leaves the stem, no matter how many bundles make up the trace. The writer has found, as a single exception to this, that in *Chenopodium Bonus-Henricus*, which possesses five bundles to the leaf trace, there are three gaps left by the departing vascular supply to the leaf. The significance of this is doubtful, and at any rate cannot be evaluated until more is known of primary systems in general. For the present, the appearance of the characters under discussion, although present in both monocots and dicots, had better be regarded as a question of parallel and independent evolution.

Summary

1. An anatomical study has been made of the primary vascular system of a number of species of Chenopodiaceae and Amaranthaceae.

2. A series of diagrams of the longitudinal course of the primary bundles in these species is presented. They set forth in an ascending series a probable method of evolution of the medullary

arrangement of bundles as found in *Amaranthus*, and possibly as found in other dicotyledonous families possessing medullary bundles.

3. It is concluded that the steps in this progression are possibly as follows: (a) the cauline bundles on either side of an entering leaf trace pass into the pith a short distance (probably due to the influence of the node), and return quickly to their normal position just under the extrafascicular cambium; (b) this condition becomes exaggerated: the cauline bundles abandon their temporary course in the pith, and become medullary throughout their course in the stem; (c) the bundles of the trace behave in a similar manner. In the earlier stages of such a development, they are also members of the peripheral ring of bundles; later their course in the stem becomes more and more extended, until they are finally completely medullary.

4. Attention is called to the belief, based chiefly upon the wide distribution of medullary bundles among various dicotyledonous families, that this bundle arrangement has probably had an independent evolution in the various groups in which it is found.

5. Based upon the nature of the primary vascular system, the two families dealt with here are considered to be closely related. This conclusion, based chiefly upon flower morphology, has already been reached by other workers.

The writer wishes to express his gratitude to Professor ARTHUR J. EAMES of Cornell University for his suggestion of this problem, and for his helpful advice and kindly criticisms throughout the progress of the investigation.

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GROWTH OF CORN AND SUNFLOWERS IN RELATION TO CLIMATIC CONDITIONS[1]

W. F. HANNA

(WITH FOUR FIGURES)

Introduction

Within recent years an extensive literature has developed relating to the nature of the growth rate in plants. Various hypotheses have been advanced, but scarcely any of them offer a full explanation of the phenomena of growth; indeed, in many cases the conclusions reached are quite contradictory.

BLACKMAN (1, 2) and REED and HOLLAND (13) have laid emphasis upon the "internal" factors which govern plant growth. They have evolved growth formulas, which, in the cases investigated, seem to explain fully the course of the plant's development, independently of any fluctuations in climatic conditions. BRIGGS, KIDD, and WEST (3, 4, 5, 7, 8, 14) have undertaken an extensive study of the whole subject of growth rate, dealing especially with the plant processes which in any way might be responsible for the particular form of the growth rate curve.

Numerous investigations have also been carried out with a view of bringing out the relationship between growth rate and such "external" conditions as temperature. Probably the best work on temperature alone has been done by LEHENBAUER (9), working with maize seedlings. In a recent monograph LIVINGSTON and SHREVE (10) have given an extensive review of the subject of environmental conditions and plant growth, and also have suggested and employed various indices which promise to be of value in the study of climate and its relation to plant growth.

In introducing new agricultural plants to any particular district, the questions of growth rate and the effect of different climatic factors in accelerating or retarding growth become of particular

[1] Report of an investigation carried out in the Department of Field Husbandry, University of Alberta.

interest. The sunflower, for example, has been recently introduced into northern districts as a forage crop, and in some respects is considered to be superior to corn. There is, however, a lack of exact knowledge as to the relative climatic adaptation of these two crops. In order to obtain such information, the following study was undertaken. Records of growth measurements, yields, and climatic conditions were kept. By a careful analysis of the data thus obtained it was hoped to derive fundamental information regarding the growth adaptations of these crops which might throw light upon their suitability to various parts of the country.

Experimentation

This work was carried out during 1920 and 1921. The general method employed was that of seeding standard varieties of *Helianthus annuus* and *Zea Mays* at a number of dates, beginning quite

TABLE I

PLAN OF SEEDING, OBSERVATIONS, AND YIELDS FOR 1920

Date of seeding	Plot	Crop	Date of appearance above ground	Days from seeding to appearance	Date harvested	Actual yield per plot (lb. green weight)	Percentage dry matter	Corrected yield per acre (tons dry matter)
May 14....	1	Corn	June 1	18	September 20	134.6	15.8	1.95
May 14....	2	Sunflower	May 25	11	September 20	350.7	14.2	4.33
May 21....	3	Corn	June 7	17	September 20	139.7	14.9	1.69
May 21....	4	Sunflower	June 4	14	September 20	368.2	14.8	4.33
May 31....	5	Corn	June 14	14	September 20	154.6	18.4	2.08
May 31....	6	Sunflower	June 10	10	September 20	405.4	14.1	4.19
June 10....	7	Corn	June 18	8	September 20	144.8	15.8	1.53
June 10....	8	Sunflower	June 17	7	September 20	387.5	14.3	3.77
May 14....	9	Corn	June 1	18	September 20	177.8	17.9	1.95
May 14....	10	Sunflower	May 25	11	September 20	451.5	15.1	4.33

early in the spring, and continuing until about the first week in June. The varieties used were Mammoth Russian sunflower, and Northwestern dent corn. The plans of seeding, observations, and yields are presented in tables I and II.

In order to measure the growth in height, ten plants were selected in each plot, and a small wooden stake was driven into the soil beside each plant, the top of the stake being level with the

surface of the ground. The sunflowers were measured from the top of the stake to the apex of the stem. In 1920 the corn was measured from the top of the stake to the highest point of the plant. With this method, however, the height was found to fluctuate somewhat with the turgidity of the leaves. This difficulty was overcome in 1921 by stretching the leaves of the corn plants upward to their full extent, and measuring from the top of the stake to the tip of the longest leaf. In 1920 measurements were taken at three-day intervals; in 1921 at two-day intervals. Figs. 1 and 2 show the mean height of the ten plants in each plot at different dates.

TABLE II

PLAN OF SEEDING, OBSERVATIONS, AND YIELDS FOR 1921

Date of seeding	Plot	Crop	Date of appearance above ground	Days from seeding to appearance	Date harvested	Actual yield per plot (lb. green weight)	Percentage dry matter	Corrected yield per acre (tons dry matter)
May 10*....	1		May 25	15	September 3	707.5	15.3	2.95
May 20.....	2		June 4	15	September 3	599.5	15.8	3.02
May 30.....	3	Corn	June 8	9	September 3	726.0	16.4	3.27
June 9.....	4		June 17	8	September 3	693.5	13.9	2.67
May 10*....	5		May 25	15	September 3	654.0	16.2	2.95
May 10.....	6		May 23	13	September 15	549.0	20.3	2.94
May 20.....	7		June 1	12	September 15	399.0	22.9	2.46
May 30.....	8	Sun-	June 3	9	September 15	502.0	21.6	2.98
June 9.....	9	flower	June 17	8	September 15	424.0	20.4	2.43
May 10.....	10		May 23	13	September 15	484.0	21.1	2.94
May 3.....	11		May 18	15	September 15	588.0	21.7	3.75

* Corn of plots 1 and 5 killed by frost on morning of May 28, and seeded again May 30; plants of second seeding appeared above ground June 8.

For the purpose of calculating the actual growth rates presented in fig. 3 for 1920, the height of the plants in plots 1, 3, and 9 of corn and plots 2, 4, and 10 of sunflowers have been averaged for each date of measurement. In 1921 the actual growth rates indicated in fig. 4 have been obtained from similar averages of plots 1, 2, and 3 of corn, and plots 6, 7, and 10 of sunflowers. The relative growth rates shown in figs. 3 and 4 have been calculated from these averages by employing BLACKMAN'S (1) compound interest formula: $\frac{R}{100}=\frac{\log_{10} H_2-\log_{10} H_1}{t\times 0.4343}$, where H_1 is the height

of the plant at the beginning of the period, H_1 the height at the end of the period, t the length of the growing period (in 1920

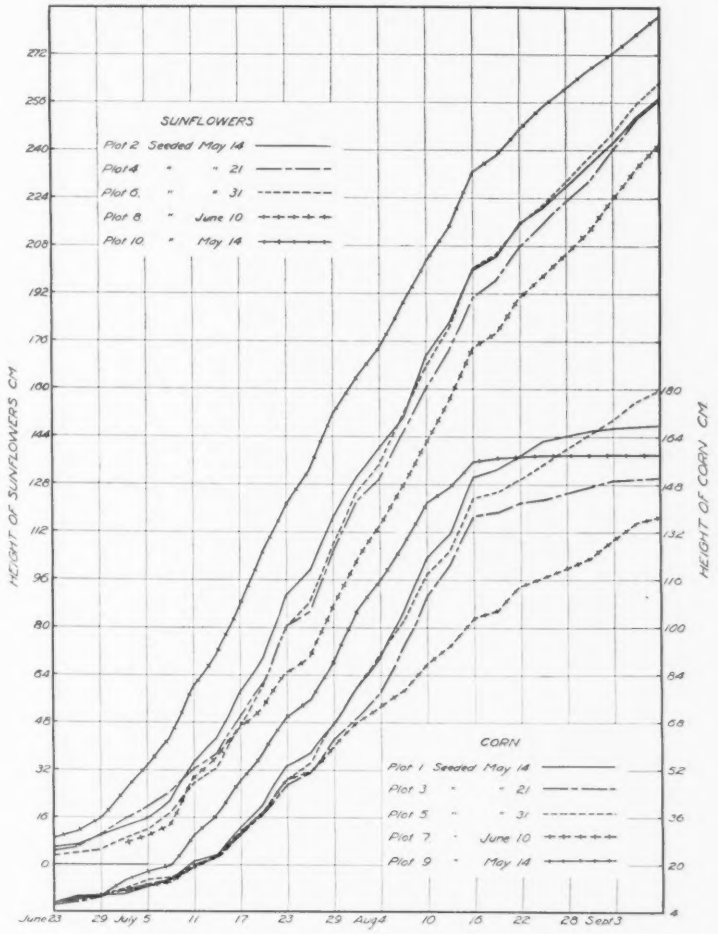
SUNFLOWERS
Plot 2 Seeded May 14
Plot 4 " " 21
Plot 6. " " 31
Plot 8. " June 10
Plot 10. " May 14
CORN
Plot 1 Seeded May 14
Plot 3 " " 21
Plot 5 " " 31
Plot 7 " June 10
Plot 9 " May 14
HEIGHT OF SUNFLOWERS CM
HEIGHT OF CORN CM
June 23 29 July 5 11 17 23 29 Aug 4 10 16 22 28 Sept 3

FIG. 1.—Mean height (cm.) of corn and sunflower plants at different dates in 1920

3 days, and 1921 2 days), and R the percentage of increase in height per day, per unit of height, for the whole period.

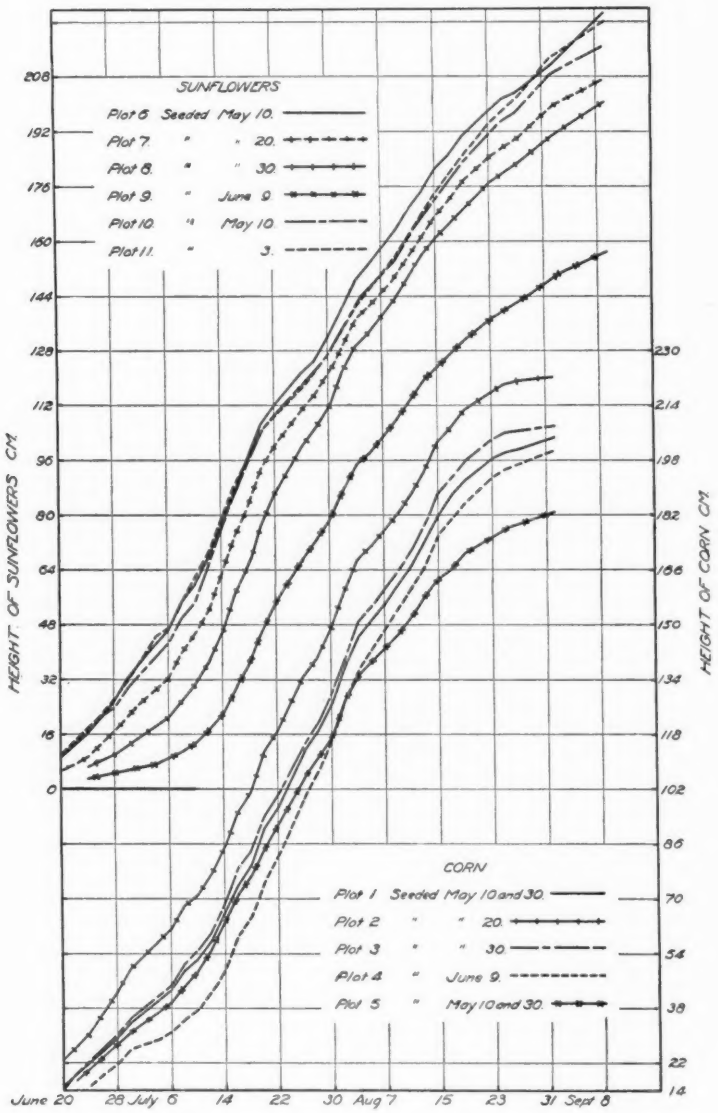

FIG. 2.—Mean height (cm.) of corn and sunflower plants at different dates in 1921

When the plots were harvested the green weight of fodder was obtained. At the same time a representative sample was taken from each plot and the percentage of dry matter determined. The corrected yields per acre, given in tables I and II, were calculated by the method outlined by NEWTON (**12**).

Temperature data for the two years were obtained from a self-recording atmospheric thermograph situated close to the plots. From these charts the mean bi-hourly temperatures have been obtained. The mean temperature for each day of the growing season was then calculated from the bi-hourly readings. In this way it has been possible to arrive at a series of values which are based not only upon the magnitude of the temperature, but also upon its duration.

Reference was made to the work of LIVINGSTON and SHREVE (**10**) in order to express temperatures in the form of the following efficiency indices for plant growth.

(1) Direct temperature efficiency indices.—This method assumes that above 0° C. the rate of plant growth is directly proportional to the temperature.

(2) Remainder temperature efficiency indices (growth at 4.5° C. taken as unity).

(3) Remainder temperature efficiency indices (growth at 10° C. taken as unity). The remainder indices are similar to the direct indices except that in each case a higher temperature has been assumed as the zero point of growth.

(4) Exponential temperature efficiency indices.—The calculation of these indices is based on the assumption that at 40° F. plant growth takes place at unit rate, and that for each increase of 18° F. (or 10° C.) above this point the rate of growth is doubled, according to the Van't Hoff-Arrhenius principle.

(5) Physiological temperature efficiency indices.—LEHENBAUER'S (**9**) data on the growth of maize seedlings at various temperatures when exposed for twelve-hour periods have been used by LIVINGSTON in preparing these indices. Plotting growth rates as ordinates, and temperatures as abscissae, a curve was obtained giving indices ranging from zero at 2° C., through a maximum of 122.3 at 32° C., to zero again at 48° C.

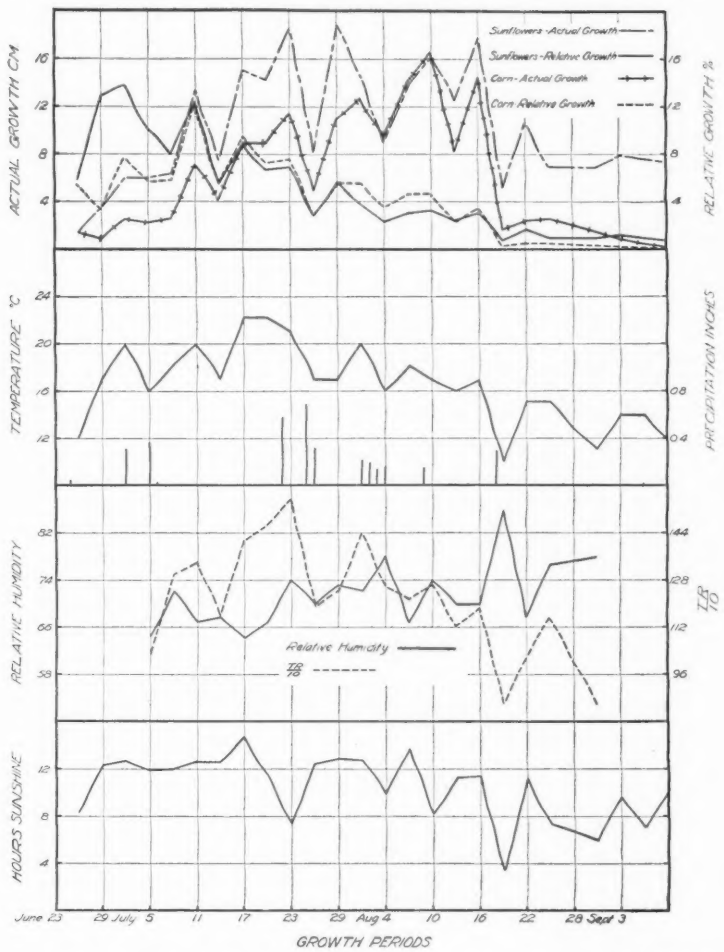

FIG. 3.—Actual and relative growth of corn and sunflower plants for three-day periods in 1920, together with mean temperature (C.), precipitation (inches), mean relative humidity, the product $\frac{TR}{10}$, and mean daily hours of sunshine for corresponding periods.

(6) Degree hours.—This method of expressing temperature indices has been used by MOSIER (11) in his study of the climate of Illinois. Considering the zero point of growth as 40° F., degree hours have been calculated for the different periods by multiplying the number of hours during which the temperature is above 40° F. by the number of degrees the average temperature is above that point.

Records were also kept of relative humidity, precipitation, and total hours of sunshine. In 1921 the maximum solar radiation was obtained from a black bulb thermometer *in vacuo*, for each day from July 4 to September 8. As high temperatures combined with high relative humidity should give conditions most favorable for rapid growth, the value $\frac{TR}{10}$ has been employed in this study as an attempt to express this condition. Here T is the mean temperature (C.) for the period of growth, and R the mean relative humidity for the same period. The large products resulting have been divided by 10 in each case. The voluminous tables of data recorded or calculated for the foregoing measurements and indices are not included in the present brief summary of the investigation. These, however, have been utilized in deriving various coefficients of correlation, some of which are reported later.

Discussion

From an examination of tables I and II, it is evident that the interval of time from seeding to the appearance of the plants above ground decreases with each date of seeding. While in the early May seedings, sunflowers have germinated much more rapidly than corn, the last seedings show little difference in this respect. No soil thermograph records were kept during 1920, but the readings for 1921 show that the soil temperature increased from 53° F. on May 14 to 65° F. on June 9. Sunflower seeds, therefore, seem to germinate with little difficulty at low temperatures, while corn germinates much more rapidly as the temperatures increase. This fact has an important bearing upon the date of seeding corn in northern districts. In 1921, by delaying the seeding from May 10 to May 30, the time required for germination was shortened

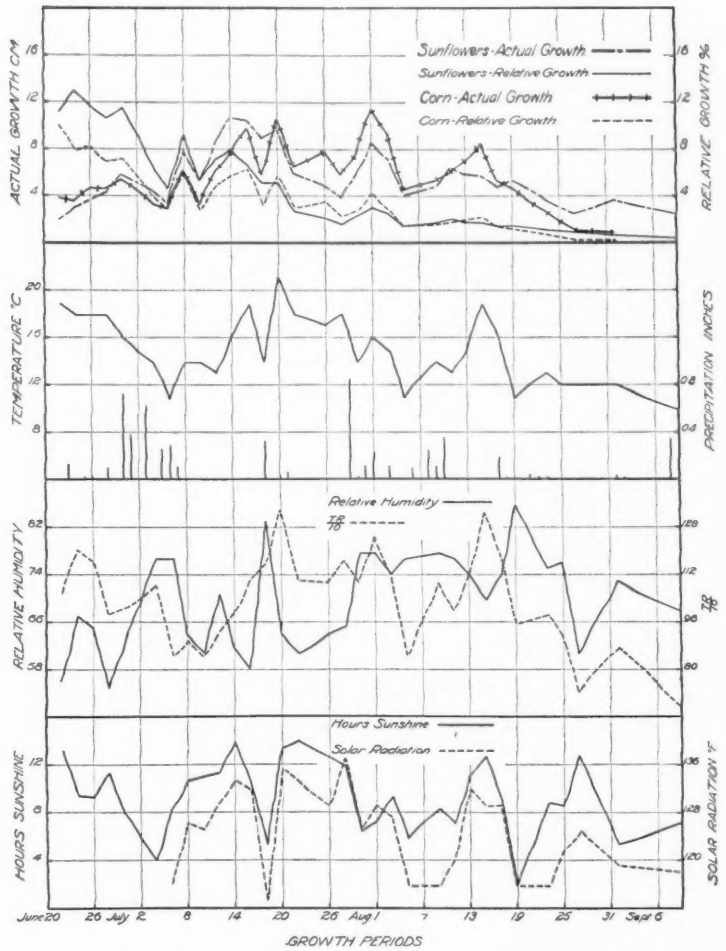

FIG. 4.—Actual and relative growth of corn and sunflower plants for two-day periods in 1921, together with mean temperature (C.), precipitation (inches), mean relative humidity, the product $\frac{TR}{10}$, mean daily hours of sunshine, and mean maximum solar radiation (F.).

by six days. In 1920 the temperature dropped to 29° F. on the morning of June 13, doing considerable injury to the first and second seedings of corn. These plants recovered, however, and a second seeding was not necessary. The sunflowers were not noticeably injured by this frost. Corn seeded on May 31 escaped this frost, as it did not appear above the ground until June 14.

In 1921 the first seeding of corn was killed by frost on May 28, when the thermometer registered 24° F. It was necessary to reseed plots 1 and 5. In this year, therefore, the earliest seeding of corn to escape frost injury was that of May 20. The sunflowers, while not killed by the frost, seemed to have suffered injury. Many plants assumed a branching form, while several of the leaves were later seen to curl slightly.

The yields of sunflowers in 1920, given in table I as tons of dry matter per acre, are about double those for corn during the same year, notwithstanding the higher percentage of dry matter in the corn. In 1921 the sunflower yields were greatly reduced, while the yields of corn increased. During the two years considerable variation in precipitation was recorded. The precipitation from September 1, 1919, to August 31, 1920, totaled 21.08 inches, with 9.15 inches falling during May, June, and July. In 1921 records for corresponding periods show a precipitation of 15.65 inches and 7.48 inches respectively. It may be concluded, therefore, that sunflowers have a relatively high water requirement. This is in harmony with results obtained by WOLLNY. In his work, reported by BRIGGS and SHANTZ (6), the water requirements of corn and sunflowers are given as 233 and 490 respectively.

From the preceding it is evident that sunflowers germinate more rapidly in the early spring than corn, and survive temperatures as low as 24° F. without serious injury. Their growth, however, is quickly retarded in dry soils.

In figs. 3 and 4 the actual and relative growth rates have been plotted, together with the climatic data for the same periods. During both years the relative growth rate is quite high at the beginning of the season, but gradually falls, and finally assumes an almost straight line, parallel to the time axis. Both actual and relative growth rates show a closer relationship with temperature

than with any of the other climatic factors. The corn seems to have made especially rapid growth at high temperatures.

Since the relation between temperature and growth seems to be so intimate, it becomes of interest to consider the coefficients of correlation for a few of the plots. The coefficients of correlation with the direct temperature efficiency indices for each date of seeding of corn and sunflowers are given in table III.

TABLE III

COEFFICIENTS OF CORRELATION (R) FOR DIRECT INDICES AND GROWTH

Date seeded	Plot	Corn	Plot	Sunflowers
	1920			
May 14	1	0.3613±0.1173	2	0.5184±0.0987
May 21	3	0.3389±0.1104	4	0.4184±0.1113
May 31	5	0.3479±0.1186	6	0.4729±0.1047
June 10	7	0.4793±0.1108	8	0.2864±0.1320
	1921			
May 10	.....	.....	6	0.6496±0.0680
May 20	2	0.4564±0.0959	7	0.4854±0.0911
May 30	3	0.4000±0.1017	8	0.5427±0.0869
June 9	4	0.4814±0.0963	9	0.4778±0.0951
May 3	.....	.....	11	0.6055±0.0664

In both 1920 and 1921 the correlations between the rate of growth of corn and changes in temperature as measured by direct indices are very slight, especially when considered in relation to the probable error. There seems to be, however, a slight increase in the correlation value as the date of seeding becomes later, the last seedings giving the highest correlations. On the other hand, with sunflowers the early seedings have given the best correlations, while the values for the later dates fall off decidedly.

In order to measure, if possible, the accuracy with which various other indices express the relationship between climatic conditions and growth, correlation coefficients have been calculated for plot 2 (1921) of corn, and plot 11 (1921) of sunflowers. These plots were chosen because they represent the earliest successful dates of seeding for the year. In addition, they gave evidence of corre-

lation with the direct indices, a form of temperature measurement commonly employed in such studies. The results are given in table IV.

The best correlation between the growth of sunflowers and temperature is obtained when direct temperature indices are employed. With the remainder indices above 10° C., and also with the physiological indices, there is no correlation whatever. The relation with hours of sunshine and the product $\frac{TR}{10}$ is very slight, while the value for relative humidity is a minus quantity.

TABLE IV

COEFFICIENTS OF CORRELATION (r) FOR PLOTS 2 AND 11 (1921)

Efficiency indices	Plot 2 Corn	Plot 11 Sunflowers
Direct indices	0.4564±0.0959	0.6655±0.0664
Remainder indices (4.5° C.)	0.5292±0.0872	0.6469±0.0693
Remainder indices (10° C.)	0.6407±0.0714	0.2571±0.1113
Exponential indices	0.4582±0.0957	0.6387±0.0706
Physiological indices	0.5798±0.0804	0.0355±0.1190
Degree hours	0.5380±0.0861	0.6207±0.0733
Hours sunshine	0.4322±0.0985	0.4100±0.0992
$\frac{TR}{10}$	0.6606±0.0683	0.3991±0.1002
Relative humidity	−0.0910±0.1201	−0.0600±0.1188

The correlation between the growth of corn and temperature is considerably better with the remainder indices of 4.5° C. than with direct indices. It is still higher with remainder indices of 10° C., while the best correlation with the growth of corn has been obtained with the product $\frac{TR}{10}$. The correlation between the growth of corn and physiological indices is comparatively good when compared with the corresponding value for sunflowers. Since the physiological indices were actually derived from LEHENBAUER'S (9) data on maize seedlings, it is not surprising to find that the corn plants in their growth show a much closer relationship with these indices than do sunflowers. It appears, therefore, that physiological temperature efficiency indices for expressing plant growth can be of little value unless derived from observations on the particular kind of plants under consideration.

Although too much reliance cannot be placed upon the correlations in table IV, there seems to be considerable evidence to show that while sunflowers make good growth at medium or quite low temperatures, corn responds most closely to high temperatures, and is particularly influenced by favorable conditions of temperature and relative humidity.

From a study of the climatic data, growth measurements, and yields for the two years, certain conclusions may be drawn regarding the climatic adaptations of these two crops. The outstanding difference in the climate for the two seasons was the low precipitation for 1921, which was accompanied by a light yield of sunflowers. Corn on the other hand showed no such reduction in yield. Sunflowers have germinated and started growth more rapidly than corn when seeded at the early dates; they have not been injured seriously by late spring and early fall frosts, and for that reason have a considerably longer growing season. Corn has been very susceptible to frost injury, and gives evidence of rapid growth at high temperatures.

Sunflowers, therefore, should be better suited than corn to those parts of the country where precipitation is ample, but where there is a short growing season with low temperatures in spring and fall, and danger of frost injury. Corn should give good results where the season is longer, temperatures higher, and where soil moisture is not sufficient for the successful culture of sunflowers.

Summary

1. During 1920 and 1921, a study has been made of the growth of *Zea Mays* and *Helianthus annuus* in relation to their climatic environment. The varieties used were Northwestern dent corn and Mammoth Russian sunflowers.

2. Early seedings of sunflowers were found to germinate and appear above ground sooner than the early seedings of corn, while the late seedings of both plants required about the same time for this purpose. Both were retarded by the low soil temperatures obtaining early in the season, but the corn to a greater degree than the sunflowers.

3. A temperature of 29° F. in the spring of 1920 injured the corn but did not affect the sunflowers. In 1921 a temperature of 24° F. killed the corn and slightly injured the sunflowers.

4. Because of resistance to late spring and early fall frosts, sunflowers have a longer growing season than corn.

5. An effort has been made to correlate the growth of corn and sunflowers with five temperature efficiency indices used by LIVINGSTON and SHREVE, as well as with degree hours, total hours of sunshine, the product $\frac{TR}{10}$, and mean relative humidity.

6. The growth of both corn and sunflowers has shown closer correlation with temperature than with any other single climatic factor. Corn gave the best correlation with temperature when remainder indices derived from temperatures above 10° C. were employed. Sunflowers gave the best correlation with temperatures above 0 °C. This indicates a greater capacity in sunflowers than corn for growth at low temperatures.

7. Physiological temperature efficiency indices derived from LEHENBAUER'S observations on the growth of maize seedlings have shown no relation to the growth of sunflowers, but have given a distinct correlation with the growth of corn.

8. Lack of sufficient soil moisture in 1921 was undoubtedly responsible for the low yields of sunflowers in that year. Corn showed no reduction in yield due to this cause.

9. Corn promises to give better yields of fodder than sunflowers in areas where the growing season is comparatively long, temperatures are high, and soil moisture is limited. Sunflowers should be well suited to sections where moisture is more abundant, temperatures at the beginning and end of the growing season low, and where there is danger from spring and fall frosts.

The writer wishes to acknowledge his indebtedness to Dr. ROBERT NEWTON, of the University of Alberta, under whose direction the work was undertaken and carried out.

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ORIGIN AND DEVELOPMENT OF VASCULAR SYSTEM OF LYCOPODIUM LUCIDULUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 323

JAMES JESSE TURNER

(WITH SEVEN FIGURES)

Comparatively few original papers have been published which deal with the anatomy of the sporophyte of *Lycopodium*. Of these, the later ones deal mainly with the structures of the fully developed stele, and only the earlier ones have discussed the origin and development of the tissues. Occasional brief references have been found, and these will be considered in their proper connection in the body of the paper.

In view of these facts, it has been the object of this investigation, in so far as was possible, to bring our knowledge of the origin and development of the vascular tissues, of at least one species, up to date. *Lycopodium lucidulum* Michx. was chosen as representative of the more primitive group of the genus. This species is too familiar to need any description, except to say that the alternating groups of sporophylls and vegetative leaves enable one to make a fairly accurate estimate of the age of any particular portion of the stem. The material for the investigation was supplied from northeastern Ohio by Professor JESSIE M. JEROME of Hiram College.

Stele

As early as 1846, NÄGELI (7), in his researches on the growing apices of plants, examined the apex of *L. clavatum*. He figures a very definite apical cell. He noted the simultaneous differentiation of the woody strands and the leaf traces, and concluded, not without considering other possibilities, that each strand passes off into a leaf trace. He refuted the impression, then current and still accepted in some places, that the vascular cylinder consists of a single bundle, and pointed out that it was made up of as many bundles as there are centers of lignification. In 1855 CRAMER

(2) studied the apex of *L. Selago*, and pointed out that there is no relation between the number of leaves in a single turn of the spiral and the number of strands making up the stele. In 1872 HAGELMAIER (3) published a series of articles in which he discussed the anatomy of the stem and the development of the apical region. His conclusion was that there is an apical group of from two to four cells that give rise to tissues of the stem. That same year STRASBURGER (8) gave an account of the apical development of *L. Selago*. His conclusion was that a single apical cell gives rise to the dermatogen and the periblem, and that one or two deeper cells give rise to the plerome. Later (9) he states that all the tissues of the stem arise from a single apical group. He figures three initials in transverse section and two in longitudinal section. Since that time, four papers have appeared on the anatomy of different species of *Lycopodium*, but they offer no considerable contribution to our knowledge of the development of the tissues (4, 5, 6, 10).

In the present investigation of *L. lucidulum*, the writer has never been able to trace the origin of the stem tissues to a single apical group, much less to a single apical cell. At the center of the apex there is a surface group of cells, numbering from three to five or possibly more, that by their activity give rise to the dermatogen and the periblem. Immediately below these is another group of about the same number which gives rise to the plerome. It is with this last group that we are concerned in the study of the origin of the stele. They divide both by anticlinal and by periclinal walls, but the anticlinal divisions are much more numerous at first. As a result, a lengthwise section of the cylinder shows a very blunt apex. The differentiation of the tissue systems is very rapid; 0.5 mm. below the extreme apex of the stem, it is possible to distinguish the groups which give rise to xylem from those which give rise to phloem. It seemed best to give names to these groups, and I have called the former prexylem and the latter prephloem. At this same level, differentiation is evident in the individual prexylem groups. The cells from which the protoxylem differentiates are much smaller and stain more deeply than those from which the metaxylem differentiates. On the other hand, those cells which, from their position, must be prephloem cannot be distinguished from the pericycle.

Throughout the entire period of development, the differentiation of the phloem lags behind that of the xylem. In material which was fixed in November, the older portion of the last summer's growth showed the first protoxylem well lignified, while the prephloem groups can be distinguished from the pericycle only by a slight difference in the intensity of the stain (fig. 1).

The usual number of xylem groups is six, although there are numerous variations, ranging from five to eight, both in the same

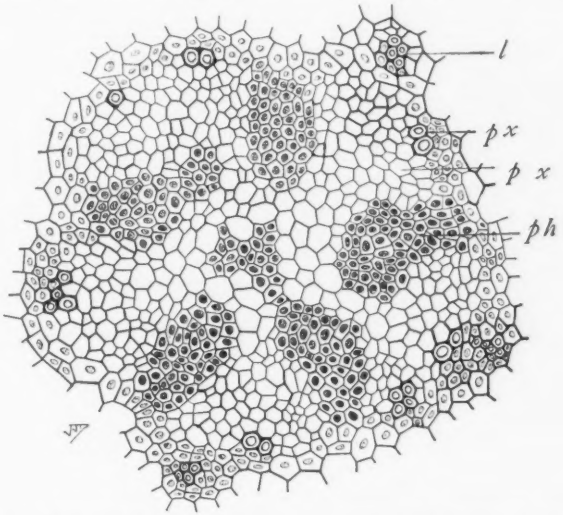

FIG. 1.—Cross-section through last summer's growth: *p-x*, prexylem; *ph*, phloem; *px*, protoxylem; *l*, leaf trace.

stem at different levels and in different stems. In some slides of sporelings, kindly loaned me by Mr. E. A. SPESSARD, the xylem groups range from two to four.

The arrangement is typically radial, the xylem groups alternating with phloem groups, and meeting more or less completely in the center. Sometimes a mass of phloem occupies the central portion. This, however, always connects with one of the peripheral bands, although in particular sections it may show as an isolated group. The differentiation of both xylem and phloem is centripetal. In my opinion the stele should be considered as a truly radial stele and not as a gamostele, either phylogenetically or ontogenetically.

In the early part of the second year, the remaining protoxylem lignifies and elongation practically ceases. The actual number of protoxylem elements is very small, if by protoxylem is meant elements with spiral or annular thickenings. From a study of developing tissues, it would seem that there is no fixed line between protoxylem and metaxylem, but that the particular type of thickening is merely a function of elongation. CHAMBERLAIN (1) calls

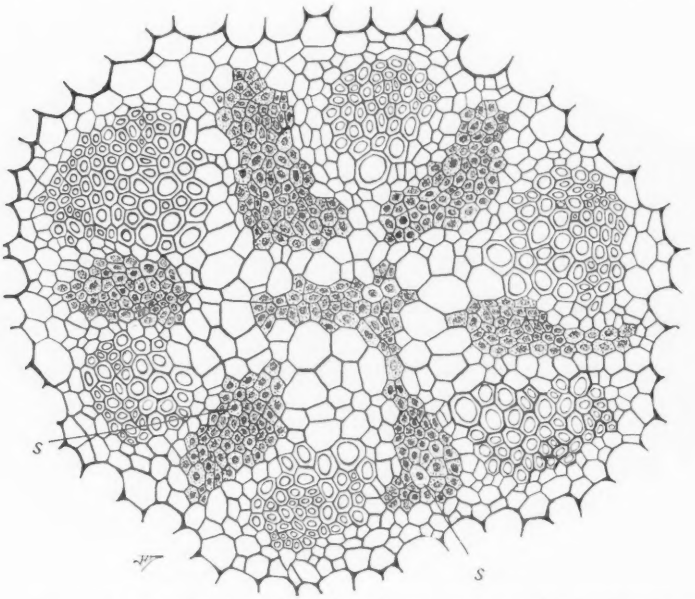

FIG. 2.—Cross-section through portion of stem two years old: lignification of xylem well along; differentiation of phloem beginning; *s*, differentiating sieve tube.

attention to pitted tracheids in what may fairly be called the protoxylem of the sporelings of *L. scariosum*. By the end of the second year, from two-thirds to three-fourths of the metaxylem is lignified. At this time occasional cells in the phloem groups show, by the lighter staining of the cytoplasm and nuclei, that they are differentiating into sieve tubes. I was not able to demonstrate the presence of any fully developed sieve tubes with sieve plates higher in the stem than the three-year old portion (fig. 2).

In the third year the lignification of the xylem is completed, and fully developed sieve tubes appear. In this particular species of *Lycopodium*, by far the larger part of the metaxylem consists of pitted tracheids; the smaller ones with uniseriate circular pits, the larger ones with oval multiseriate pits. Scalariform tracheids occur, but they are few in number. It is probable that the scalariform tracheids are a modified form of the pitted tracheids, in which

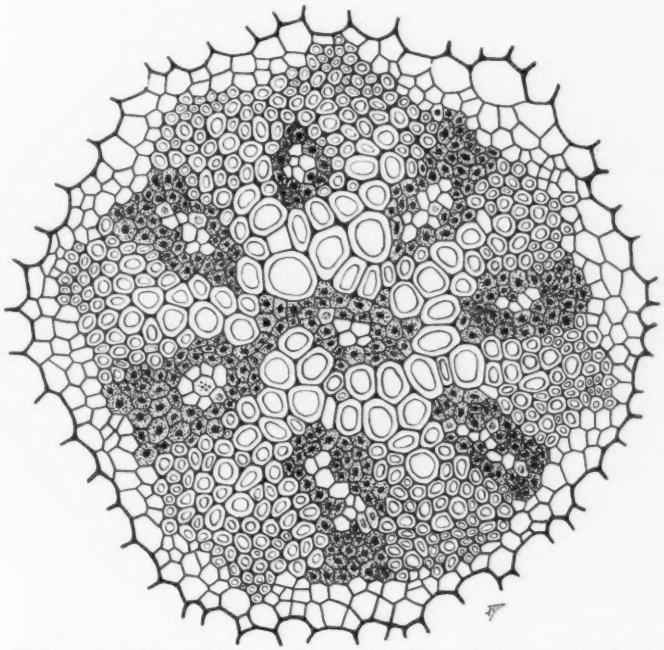

FIG. 3.—Section through three-year old portion of stem, showing completed stele

the pits are extremely elongated. Tracheids were seen which were pitted at one end and scalariform at the other, with a transition between the two forms of thickening.

The sieve tubes occupy a narrow strip in the central portion of the phloem. I could not determine that there was any definite order in their differentiation. Sometimes the first tube appeared close to the outer edge of the phloem, and sometimes close to the center of the mass. The sieve plates are scattered over the walls, and vary greatly in size (fig. 3).

Leaf strand

The leaf primordium starts as a single cell. This cuts off lateral cells and then a basal cell, but the resulting leaf is not wholly a product of these cells. The initiation of growth in the primordium seems to act as a stimulus to the surrounding tissues. Cells are activated on all sides, extending as far on the outside as the base of the preceding leaf. As a result, at the apex of the stem the leaves succeed one another without any visible length of stem intervening. It is only by the later elongation of the stem that the leaves are separated. This accounts for the decurrent leaf bases of the mature leaves (fig. 4).

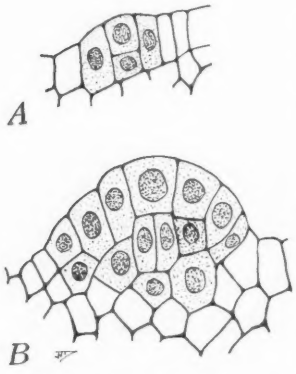

FIG. 4.—Leaf primordium: *A*, first divisions; *B*, involving of deeper layers in development of leaf.

The activation proceeds downward from the base of the developing leaf, involving deeper and deeper layers of cells. The progression in this direction is much slower, and does not reach the stele until some time after the desmogen strand is well differentiated in the leaf base (fig. 5).

The differentiation of the desmogen strand, by repeated longitudinal divisions without the transverse divisions which occur in the adjacent cells, is first evident in the base of the leaf primordium. The progression is, from this time on, both acropetal and basipetal. Acropetally, it just about keeps pace with the growth of the leaf; it never quite reaches the apex. The tip of the mature leaf is without vascular elements. Basipetally, the differentiation of the desmogen strand progresses toward the desmogen strand of the stele, meeting it some distance down the side, at an acute angle. The primordium arises without any reference to the location of the protoxylem groups. In the downward differentiation, if the desmogen strand happens to be opposite a phloem group, it swings to one side and joins with the adjacent protoxylem group. The lignification of the foliar strand proceeds in the same way.

The first thickening appears in the cells of the leaf base. By the time the first vessel has joined with the stele, lignification has begun

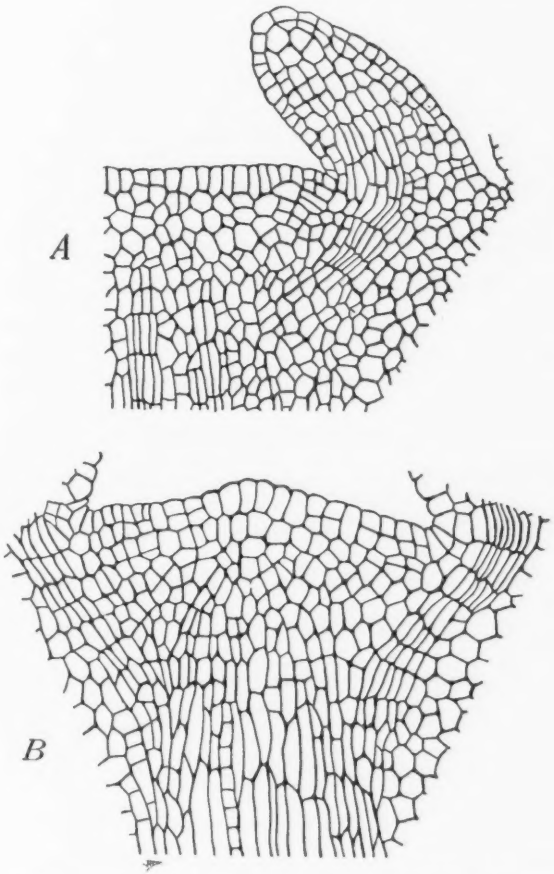

FIG. 5.—Developing strand of leaf: *A*, strand in leaf base only; *B*, connecting of strand with stele.

in other elements in the leaf base. Considerably more lignification takes place in the leaf and upper portion of the leaf trace than in that part of the trace which makes connection with the stele. A

cross-section of the leaf trace well out in the cortex shows about twice as many lignified cells as the same trace after it has passed through the endodermis of the stele (fig. 6).

The differentiation of the bundle itself begins in the center. The first lignified cell does not always occupy the exact center of the bundle, but always, so far as could be observed, within one or two cells of it. The lignification proceeds outward about equally in all directions, and is complete before the end of the first year.

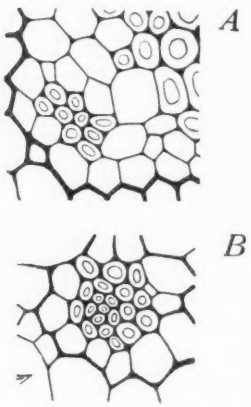

FIG. 6.—Two sections of same leaf trace: *A*, just inside endodermis of stele; *B*, 0.5 mm. outside endodermis and 1.5 mm. higher up in stem.

All of the lignified elements have spiral thickenings. In macerated preparations some of these were found to be true vessels and others tracheids. Some of these tracheids were very short, being about ten times as long as wide. No cells could be found in the leaf bundle proper or in the leaf trace that could properly be called phloem. In leaves less than one year old there was no well defined endodermis, but there was a sharp line of demarcation between the tracheids and the abutting cells. In the two-year old leaves the endodermis was well defined. In leaves older than this the thickening of the adjacent cells was extended from one to two cells farther out. The endodermis is continued in the leaf trace, but disappears as the trace passes through the endodermis of the stele (fig. 7).

Discussion

At the present time there are two views regarding the number of categories which should be made of the parts of the plant body. The older view, and the one most generally held, is that the plant body should be divided into roots, stem, and leaves. The more recent view is that the plant consists of roots and leaves. This latter ground is taken on the interpretation of the stele as being composed of leaf traces. In other words, the stem is made up of aggregated leaf bases. Whether this interpretation is justifiable

in phyllosiphonic plants, I cannot say. The scope of this investigation does not permit of an answer, but probably those who take this view disregard the telescoping of the stem which is so common in the higher plants. From this study of *Lycopodium* as a representative of cladosiphonic plants, however, I am convinced that this interpretation for this group is not supported by the facts. In *Lycopodium* the very primitive radial stele is mapped out in

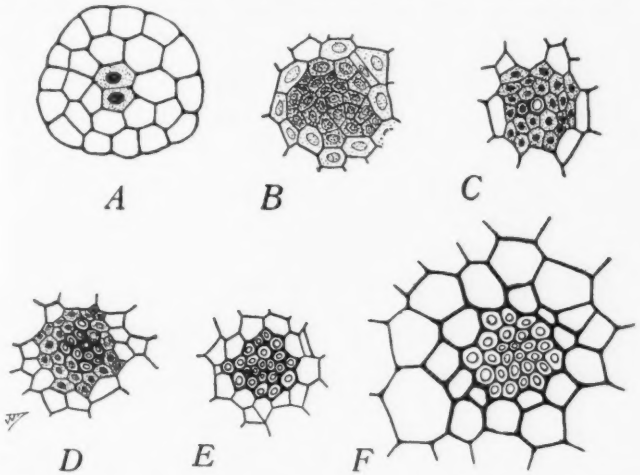

FIG. 7.—Cross-sections of leaf bundle in different stages of development: *A*, beginning of desmogen strand in primordium; *B*, desmogen strand practically completed; *C*, beginning of lignification, showing mesarch character of bundle; *D*, bundle partially lignified, showing outward progression of process; *E*, bundle completely lignified but with no endodermis; *F*, bundle from two-year old leaf with well defined endodermis.

the sporeling from the beginning, and continues to develop from an independent group of meristomatic cells so long as the plant continues to grow. This continuous stele is interrupted only by branches, and these originate by a division of the independent apical group. The vascular system of the leaves originates independently of the stele, and connects with it only by a differentiation of cortical elements. *Lycopodium*, at least, has a stem.

On the other hand, it seems that too much stress has been laid on the necessity of exactly delimiting the categories. They should

be considered as composite parts of a unified whole, rather than as separate parts making up a whole. To illustrate, the major part of the leaf trace, in its origin, belongs to the stem; but through differentiation it becomes, to all intents and purposes, an integral part of the foliar system. It may be considered as either stem or leaf, or as both stem and leaf. The same may be said for the outer layer of the cortex. By origin, it is stem; by activation, due to the formation of leaf primordia, it becomes leaf; by subsequent elongation, it again becomes a part of the stem. Where does it belong?

The direction of the differentiation in the leaf trace is a subject which deserves more attention than has been given to it. No positive statement has been found in the literature that the differentiation proceeds in either direction. Various writers speak in a vague way of the leaf trace entering the stele or passing out into the leaf; apparently the use of the terms depended upon the subject under discussion. When speaking of the stele, the leaf trace passes out; when speaking of the leaf, the trace passes into the stele. The fact is the trace passes neither in nor out. The cells composing it are laid down in place as a result of divisions in meristematic cells. The progress of the differentiation of these cells may be either in or out. In *Lycopodium* the differentiation begins in the leaf base and passes in toward the stele. What it may do in the other groups of plants is not clear from any evidence discovered in the literature on the subject.

Summary

1. The central cylinder originates independently of the leaf traces from a group of meristematic cells situated just below the apex.

2. The central stele is an exarch radial protostele consisting of alternating plates of phloem and xylem.

3. There is no sharp differentiation between the protoxylem and metaxylem, the later-forming protoxylem having the structural characters of metaxylem.

4. The differentiation of the phloem proceeds much more slowly than that of the xylem.

5. The desmogen strand of the leaf originates independently, from a group of cells in the base of the leaf primordium. Only at a later period does it join the stele by a differentiation of cortical elements.

6. The foliar bundle is mesarch, and is made up exclusively of spiral elements.

The writer wishes to express his appreciation and gratitude to Dr. W. J. G. LAND for advice and criticism, and particularly for his kindly encouragement during the progress of the investigation.

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CLOGGING OF STOMATA OF CONIFERS IN RELATION TO SMOKE INJURY AND DISTRIBUTION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 324

J. B. RHINE

Introduction

When an area of vegetation is invaded by coal smoke, the first of the higher plants to succumb to its destructive effects are the conifers. This has been attributed to the fact that the conifers are exposed all the year, and that the smoke is usually worst during the winter. In view of the fact, however, that conifers are more susceptible than other evergreens, and the deciduous European larch is more sensitive than deciduous foliage trees, mere length of exposures will not explain the situation. The explanation which has received the most support is that this higher susceptibility of the conifers to smoke injury is due to the deeply sunken stomatal pits and their tendency to catch soot and tars, thus becoming clogged. This claim was made by BAKKE (1), who attempted to estimate quantitatively the foreign material present by washing the needles with ether. He states as follows:

> On account of their deeply sunken stomata the conifers are more susceptible to smoke injury. . . . . In cross-sections of conifer needles from a smoke region the stomata were found to be at least partially filled with a tarry compound.

The most extensive work supporting this theory is that of the Leeds group, investigating smoke injury in the neighborhood of that city. RUSTON and CROWTHER (10) reported that conifers were especially sensitive to smoke. They stated that some leaves had as high as 80 per cent of the stomata blocked by soot and tar. COHEN and RUSTON (3) and CROWTHER and STEUART (5) referred to the clogging effect of soot on evergreen vegetation. RUSTON (9) stated that "80 per cent of the stomata of firs grown in the city of Leeds were found clogged by tar." COHEN and RUSTON (4) showed drawings of the stomatal pits of fir and juniper needles

with heavy black deposits overlying the guard cells. SMALLWOOD (12) found over 85 per cent of the stomata of pines growing in Washington Park, Chicago, were clogged by soot by the first of August.

In view of these reports, the claim of CLEVENGER (2) that only a small percentage of the stomata are clogged in smoke injury cannot be considered correct. He found, however, as did STOCKHARDT (13), that applications of soot alone to young firs did not produce any apparent injury to them, although slight injury was caused to the older needles of young Jack pines.

Investigation

With this work in mind, Dr. WILLIAM CROCKER, Director of Boyce Thompson Institute for Plant Research, suggested an investigation of the internal physiological condition resulting from this clogging of the stomata by soot. The work was undertaken in the fall of 1922. Smoke injured needles were taken from Austrian pines growing in Washington Park, Chicago, cross-sections made of them, and these, mounted in water, were examined microscopically.

It was found at once that every stoma was clogged, that all were overlain by a black, tarry-looking mass which certainly looked like foreign material collected in the deeply sunken stomatal pits. Even when the chief part of the deposit had been carried away by the sectioning blade, examination showed particles still adhering to the walls of the pit, indicating that the black deposit had once been there. The clogging substance filled at least half of the stomatal pit in the case of the Austrian pine, although if the section were thick it appeared to fill the whole pit. Curiously enough, however, the black color disappeared when alcohol was added to the slide, and small bubbles passed off at the same time, leaving the deposit a very light brown. This was found to be soluble in ether and xylol. Other material was then examined which had not been exposed to smoke, such as greenhouse grown conifers, nursery stock, needles collected in the mountains, etc., and the black deposit was found to be present in all, regardless of habitat. It had to be concluded, therefore, that the substance under investigation was not soot, tar, or any other foreign material, but instead was a natural product of the conifer itself.

Further examination of the literature with the new situation in mind revealed the fact that the presence of this natural deposit in conifer stomata had been noted as early as 1827 by LINK (6), had been reported by SCHLEIDEN (11), had been investigated to a considerable extent by ZUCCARINI (18), THOMAS (14), WILHELM (16), MAHLERT (7), and WULFF (17), and was mentioned in such texts as PFEFFER's *Pflanzenphysiologie* and HABERLANDT's *Physiologische Pflanzenanatomie*.

LINK, SCHLEIDEN, and THOMAS called the deposit a resin, while ZUCCARINI, WILHELM, MAHLERT, and WULFF claimed it was a wax. Alcohol was the reagent upon which these conclusions were based, in the main. It is not surprising, therefore, that there should be some disagreement, since it is difficult by this means alone to distinguish between wax and resin microchemically. There are more modern tests, however, that readily distinguish between waxes and resins. Chloral hydrate will dissolve resins but will not dissolve waxes. Concentrated sulphuric acid will dissolve resins, producing a brown color, but will not dissolve waxes (15). These tests were made on the stomatal deposits of Austrian pine, two species of juniper, and three of fir. In all cases examined the deposit was found to be a wax and not a resin. It appeared to be the same substance that occurs on the under side of the needles of many conifers; and in the needles which had both the wax deposit in the stomata and the coating on the surface of the leaf, the two seemed continuous. This was first pointed out by WILHELM.

The wax appears granular under high magnification, and is evidently porous, since air bubbles are seen to escape from the deposit when alcohol is added to a cross-section previously mounted in water. This air is not driven out by cold water, because of its lower penetrative power, and the air having a lower refractive index than the water appears black, and gives the wax granules the appearance of soot. Furthermore, the need for this route as a channel for gas exchange in the conifer needle does not allow any other conclusion than that the wax is penetrated by gases.

While gas exchange is possible through this deposit of wax, undoubtedly it is very much retarded. The wax must form a "damper" on the processes of respiration, transpiration, and

photosynthesis, protecting the tree against excessive water loss and reducing the rate of metabolism. If this be true we should expect that trees having this protecting wax would be able to live in more xerophytic conditions, while those lacking it, other things being equal, would be confined to the more moist regions. It is true that we cannot determine to what extent "other things are equal," and therefore cannot ascertain the exact value of this stomatal deposit as a factor in conifer distribution, but there can be no doubt that it is a factor of considerable importance.

In support of this view, the following interesting parallel between xerophytism and the presence of stomatal wax in the conifers is pointed out. The conifers reported to have wax in their stomatal pits are *Abies* spp., *Picea*, *Juniperus*, *Cedrus*, *Thuya*, *Pinus*, *Cupressus*, *Chamaecyparis*, *Larix*, and others of the Abietineae and Cupressineae. These wax-containing conifers for the most part are xerophytic, and either inhabit dry regions or the "physiologically dry" conditions of northern latitudes, where the frozen soil of winter affords very little moisture. *Abies* and *Picea*, which advance farthest into this latter condition, have very heavy deposits of wax. The piñon pine of the arid southwest likewise has an extremely large amount of stomatal wax. On the other hand, the following conifers, which are well known as moist habitat trees, and which are confined to moist temperate or tropical rain-forest conditions, do not have the deposit of wax in their stomatal pits: *Araucaria*, *Dammara*, *Podocarpus*, *Torreya*, *Taxodium*, and *Taxus*. *Ginkgo*, as a close relative, might be mentioned in this group as not having the wax. *Pinus cubensis* was found to be without the stomatal deposit. We can hardly avoid the conclusion, therefore, that this wax deposit affects the moisture requirement, and consequently the distribution of the conifers that have it.

Since the stomatal deposit is not soot, the relation between smoke injury and the conifer stomata is not so obvious. In fact, there is much question whether there exists any such relation at all. PFEFFER (8) thought the "resin" (he referred to the work of THOMAS) might catch soot and dust, and hold enough foreign material on its surface to close its pores. It is true that the wax deposit in the stomata of needles exposed to dust and smoke does

have a thin film of foreign substance over its outer surface, and this film does not disappear in alcohol. In fact, the whole surface of the needle becomes coated with soot during the winter in smoky regions. The addition, however, of more particles to the granular wax deposit could only make the retarding layer a trifle thicker, at worst. If the air pollution includes tarry and oily substances, it might well be that in time these would close the pores of the sievelike layer of wax, but the adhesive particles would certainly clog the tiny stomatal slits themselves, where there is no wax overlying, more readily than the larger expanse of wax. Moreover, if such clogging were the nature of the injury, STOCKHARDT and CLEVENGER should have obtained injury to fir trees from their heavy applications of soot, especially since fir has much wax.

As a factor affecting the moisture relations of the conifers, however, the stomatal wax may have some bearing on their higher susceptibility to smoke injury. It is well known that the trees most resistant to smoke injury are the willow, cottonwood, elm, elder, alder, sycamore, tulip tree, catalpa, white poplar, aspen, etc. These are trees using considerable water, having a rapid growth rate, and are found usually in river bottoms and moist meadows. The slow growing trees of dry habitat do not so well withstand the ravages of smoke. The conifers mostly grown in cities of this latitude stand at the extreme of this class, that is, they are xerophytic. Yew and cypress are the more resistant and are also the more mesophytic. They have no stomatal wax. In general, there seems to be some relation between the natural moisture requirement of the conifer and its resistance or sensitiveness to smoke. At present, however, it can only be ventured as a suggestion.

Summary

1. The black deposit found in the stomatal pits of certain conifers, and thought to be soot, was found to be a natural product of the leaf.

2. The substance in the stomata of juniper, fir, and Austrian pine was found to be a wax.

3. The wax is finely granular, permeable to gases, but must greatly retard gas exchange and thus retard metabolism and water loss.

4. There is a remarkable parallel between presence of the wax and xerophytism in the conifers, and between absence of the wax and mesophytism (and hygrophytism).

5. No relation is seen to exist between wax in the stomata and the high sensitiveness of certain conifers to smoke, except that as a factor inducing xerophytism the wax may lower the resistance of the tree.

The appreciative interest and helpful criticism of Professor HENRY C. COWLES are responsible for the assembling of this material for publication. Dr. GEO. D. FULLER very kindly furnished material and information.

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18. ZUCCARINI, J. G., Beiträge zur Morphologie der Coniferen. Abhandl. Math.-Phys. Classe Bayerisch. Akad. Wissen. **3**:788–790. 1843.

BRIEFER ARTICLES

VARIATION IN VIGOR OF SPROUTS FROM QUARTERS OF SINGLE TUBERS[1]

(WITH ONE FIGURE)

In the course of a physiological study of the potato plant, an attempt was made to secure four uniform groups of plants for four distinct treatments by quartering seed tubers. Thus each tuber would produce four plants, or groups of plants, and the plants under one treatment would be from the same original tubers as those under any other treatment. To keep all conditions as uniform as possible in starting the plants, Early Ohio tubers from cold storage were quartered along the longitudinal axis. Each seed piece was trimmed along a cut face until it weighed between 25 and 30 gm. (approximately 1 ounce). Each piece was then planted in a pot in ordinary soil that had been thoroughly mixed. They were carefully planted in the same position, each piece being placed horizontally, about two inches deep, with the uncut surface up. Thirty tubers were thus quartered and planted. As the plants were not to be subjected to the different treatments until they were of a measurable height, the pots were labeled and placed together under uniform greenhouse conditions.

In spite of the precautions in cutting and planting the seed piece, there was a marked variation in the time of appearance above the soil of the sprouts from the four pieces of the same tuber. There was an equally striking variation in the vigor of sprouts; the more vigorous sprouts in general being first to appear. As the tubers were relatively dormant when planted (early in April), most of the seed pieces produced only a single sprout. The weak, slow growing sprouts were an exception to this, for they were soon followed by still smaller secondary sprouts.

The variation was so consistent throughout the entire experimental planting, that the plants from six original tubers were examined at this stage. The seed pieces were found free from rots or other injuries. The young plants were vigorous and free from diseases, insects, or the effects of soil deficiencies. Typical plants from two quarters of the

[1] Published with the approval of the director as Paper 432 of the Journal Series of the Minnesota Agricultural Experiment Station.

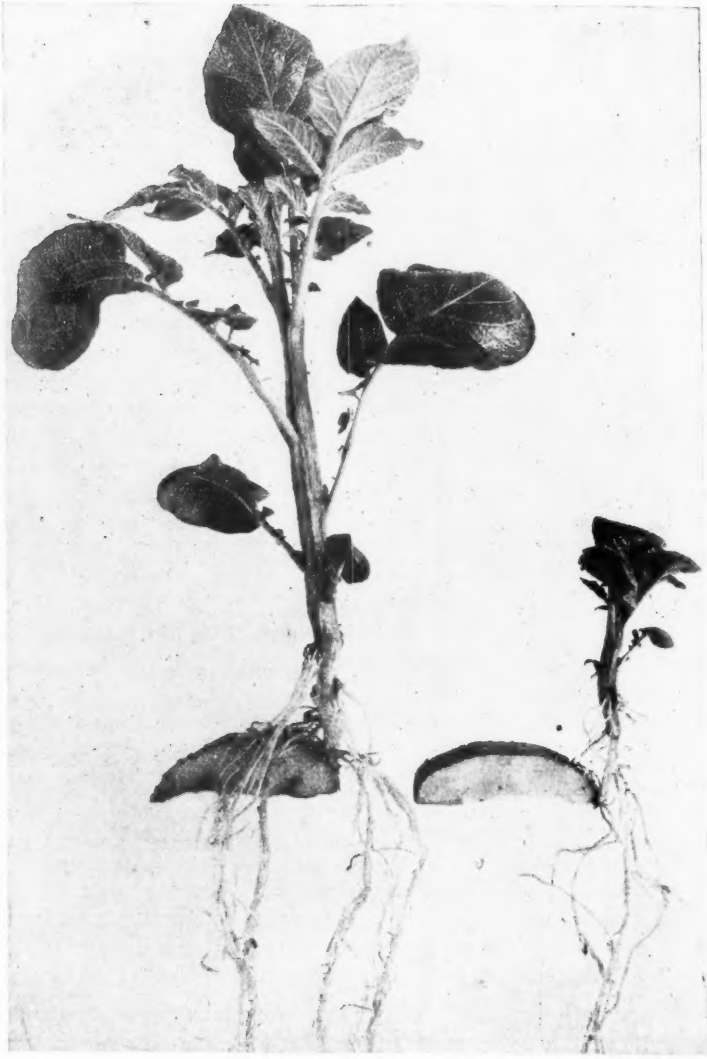

FIG. 1.—Variation due to position of sprout on seed piece; part of seed pieces cut away to show point of attachment.

same tuber are shown in fig. 1. It may be noted that the sprouts have arisen from eyes near the bud end, a condition which held in all those examined. As the seed pieces tapered toward the bud end, some of the sprouts were attached at the extreme tip. In all these cases the plants were very small. This condition was found to hold generally; that is, all of the small plants were attached at the tip or near the edge of the seed pieces, while the larger plants had arisen from more centrally located buds. A part of the seed piece has been cut away to better illustrate this. The vigor of the sprout was directly correlated with its position on the seed piece. Plants arising near the edge or at the tip apparently were unable to draw upon the reserve foods of the tuber as successfully as sprouts more favorably located.

The remainder of the experimental plants were divided into four lots according to the original plan. In each lot there was a wide variation in size of plant. Frequent measurements were made on these plants up to the period of tuberization. The stronger sprouts consistently produced the larger plants. As the experiment was discontinued at the time of tuber setting, there is no direct evidence from these data that the more vigorous plants would have produced the larger yield. STEWART,[2] however, has presented some evidence on this point. He measured the height of plants in the field when ten inches or less in height, and found an excellent correlation between height of plant at this stage and final yield. From this evidence it seems safe to conclude that the effect of the sprout's position on the seed piece is carried through the growing season, and to a degree affects the yield.

In an earlier paper STEWART[3] reported in detail variations from halves of the same tuber of the same magnitude as the variations found in the present work. He was unable to account for the differences he observed. As the variations between hills from halves of the same tuber were entirely comparable with the variations from the quarters found here, they may have been due largely to the position of the sprouts on the seed piece. This conclusion, however, perhaps is not entirely justified, for STEWART was dealing with seed pieces that produced four to six sprouts. It would seem that several sprouts would draw more uniformly on the food reserves of the seed piece than single sprouts, and

[2] STEWART, F. C., Potato seed experiments: whole small tubers vs. pieces of large tubers of the same plant. New York Agric. Exp. Sta. Bull. 491. 1922.

[3] ———, Further studies on the effect of missing hills in potato fields and on the variation in the yield of potato plants from halves of the same seed tuber. New York Agric. Exp. Sta. Bull. 489. 1921.

the variations between such groups of sprouts due to position on the seed piece could hardly be as great as in the single sprouts of the present study.—JOHN BUSHNELL, *Ohio Agricultural Experiment Station, Wooster, Ohio.*

THE SMEAR METHOD FOR PLANT CYTOLOGY

Cytological students of the maturation divisions in animals for some time have enjoyed the advantages of the "smear method" of preparation of tissues, by which the material is spread in a thin film on a cover glass, fixed, stained, and mounted *in situ*. The resistant united cell walls of plant tissues would seem to preclude the use of this technique in botanical practice, but it is obvious that this condition is absent during all but the earliest stages in pollen development, which perhaps of all plant phases has received, yet still needs, the most critical study. The only botanical adaptation of the "smear method" of which the writer is aware is the use of the aceto-carmine method, especially as advocated by BELLING, a method of undoubted value where a prompt report on the progress of the main meiotic phases or on the chromosome number is all that is required. This method produces a comparatively fugitive product, however, and the mounting medium (acetic acid) is of a refractive index low enough to introduce difficulties in the precise use of oil immersion objectives. In the writer's experience the method has not been favorable for a study of spireme conditions, and even in metaphase and anaphase has caused some distortion and swelling of the chromosomes.

The "smear method," however, may be so conducted that the product can be mounted in balsam and kept indefinitely. The fixing fluid used is a chrom-osmic-acetic mixture of the following constitution: 10 per cent acetic acid 2 cc.; 10 per cent chromic acid 0.2 cc.; osmic acid dissolved to 2 per cent strength in 2 per cent chromic acid 1.5 cc.; distilled water 8.3 cc. About 1 per cent of maltose has usually been added to this fluid, which will probably have to be modified to suit each plant on which it is used. A slender glass rod is laid in the bottom of a Petri dish, and enough of the fixing fluid poured in to cover it. It has been found more convenient to use slides than cover glasses, and these are cleaned by long immersion in battery fluid, rinsed, and dried with an absolutely clean cloth. The anthers are excised, and as soon as collected are crushed and spread over the center of the slide with quick strokes of a clean scalpel, which must be honed flat and smooth on the face or

the smear will not be a success. The slide must be immediately inverted on the fixing fluid, bringing it down in a horizontal position, so that the whole smeared face is wet simultaneously. The time from the first crushing of the anther to fixing should not exceed 3–5 seconds. If the slide is brought down on the fluid in an oblique position much of the material will wash off. The slide may stay in the Petri dish, resting on the glass rod, for a few moments, while a second is prepared and placed beside it; then it may be removed, turned right side up, flooded with the fluid, and left for the full time of fixing, or about 15 minutes. The slides are then to be washed in changes of water in staining wells for about an hour, and any large pieces of anther walls, filaments, etc., which have not broken loose, can be picked off with a needle. A preliminary inspection of the material can also be made, and slides showing stages which are not desired may be discarded. The developing pollen mother cells adhere excellently, and rough rinsing does not dislodge them. Smears of pollen grains are quite easily made, so long as they are still surrounded by viscous fluid in the anther, and a very fair fixation may be secured through the chitinous wall, so that the first mitosis within the pollen grain may be critically studied.

If the slides are to be stained at once, they are then bleached in diluted aqueous hydrogen peroxide, rinsed again, and placed in 2 per cent iron ammonia alum solution; or they may be partly dehydrated and held in 70 per cent alcohol for later staining. After 4–12 hours in the iron alum they are again washed most carefully for 15 minutes or more in running water, and stained for 4–12 hours in 0.5 per cent aqueous haematoxylin solution, followed by another rinsing, destaining under observation in the iron alum, and an hour of final washing. Dehydration is to be accomplished gradually through alcohols by 10 per cent stages, but the slides need remain in each stage only 2–3 minutes. Clearing must be done by mixtures of xylol and absolute alcohol, of which about four intermediate stages seem to be enough. In this connection it must be noted that the somewhat mucilaginous walls of the developing pollen mother cells are intact, and as a result any great change in the density of the successive solutions into which the slides are introduced is sure to cause collapse of the walls and shrinkage of the protoplast. After the smears have come from pure xylol, very dilute xylol balsam is dropped on them and allowed to concentrate by drying for a few minutes before the cover glasses are put in place.

The chief difficulty encountered is that of getting a brilliant stain, but the writer has eventually succeeded in doing so in those plants

which he has so far tried. The haematoxylin and iron alum must both be of the best grade and in good condition, but in spite of care some batches of slides will show a muddy stain. Passable results can be secured within a single working day by shortening the staining periods, thus enabling chromosome count work to be done very rapidly, with the advantage over the aceto-carmine method of permanency of the slide records. Because the cells are spread out in a single layer and in immediate contact with the fixing fluid, the quality of the fixation may be very high. The karyolymph is precipitated in a uniform and delicate way, giving the much desired "solid fixation" of the nucleus, as a result of which the chromatin elements retain their normal position within the membrane, resisting the tendency to clump at various stages so familiar in paraffin material. The cells further are entire, and the observer may work without the necessity of accounting for parts of one cell displaced into two or three sections. This is not always an advantage, but in making chromosome counts it is much to be desired, and this method gives entire metaphase plates without broken or cut chromosomes. It might be thought that the making of the smear would rupture the pollen mother cells, or at least displace the contents within them, but it is found that most of the cells escape damage, and in the others it shows so obviously that there is almost no possibility of confusing normal and abnormal conditions.

The writer's experience with this method has been almost entirely limited to monocotyledonous plants, as *Gasteria* and *Velthemia*, but from random observations and the experience of his students he is confident that it will serve for many dicotyledons also. It will probably succeed best when there is a large amount of archesporial tissue and a minimum of reserve food in the developing pollen mother cell.— Wm. Randolph Taylor, *University of Pennsylvania.*

THE HOLDFAST OF CHAETOMORPHA TORTA

(WITH ONE FIGURE)

Chaetomorpha torta (Farlow) McClatchie, one of the largest members of the genus, is frequently washed ashore on the coast of southern California; it is usually found as curled, tangled masses conspicuous by the peculiarly glassy appearance of the dark green filaments. During the period of January to May, 1923, the writer examined hundreds of these

tangled filaments without noting a specimen with holdfast intact. SETCHELL and GARDNER[4] have written in this connection as follows:

> In searching for any trace of an attachment, our persistence was rewarded by the discovery of one among all the material examined, and that, curiously enough, was found on no. 211 of FARLOW, ANDERSON, and EATON's *Algae Americae Borealis Exsiccatae*. The rhizoids are slender, blunt, somewhat branched, and evidently were attached to a rock surface.

FIG. 1.—Holdfast of *Chaetomorpha torta* (Farlow) McClatchie; ×40

On February 2, 1923, while searching for lobsters under partially submerged shelving rocks a short distance north of the Scripps Institution for Biological Research, the writer felt a mass of slippery filaments attached to the under surface of a flat rock. They were typical specimens of *C. torta*, except that the filaments were almost straight while attached to the rock. Upon being removed from the rock they immediately became coiled and twisted, after the manner of the masses found along the shore. A number of specimens were carefully removed from the rocks with little injury to the holdfasts. One of these, shown in fig. 1,

[4] SETCHELL, W. A., and GARDNER, N. L., The marine algae of the Pacific Coast of North America. Part II. Chlorophyceae. Univ. Calif. Publ. Botany **8**:199–206. 1920.

was photographed at once. The holdfasts withered quickly and were not easily studied on the specimens after drying. It will be noted from the figure that the rhizoids are relatively large where they branch from the main filament, and that they are considerably branched. These points are in contrast with the description by SETCHELL and GARDNER; the fresh material undoubtedly permitted of more satisfactory examination than did the one herbarium specimen mentioned in their description.

In discussing the habits of *C. torta* and *C. spiralis* Okam., SETCHELL and GARDNER use the terms "erect and tufted" for one group of members of the genus, and the terms "prostrate or flexuous or crisped habit, intertwining and becoming detached" for another group. The writer suggests that the habit of *C. torta* might be described as pendent in locations such as that described in this article. It seems possible that the curled and contorted habit of detached specimens may be due to the release of tensions which serve to keep the filament almost straight while it is attached to the rock.

The writer is indebted to Dr. N. L. GARDNER for confirming the identification of *C. torta*.—ORVILLE TURNER WILSON, *University of Cincinnati*.

CURRENT LITERATURE

BOOK REVIEWS

Beneke-Jost Plant Physiology

The exhaustion of the third edition of JOST's *Lectures on Plant Physiology*, which appeared about ten years ago, has led to the revision of the text by the author, with the collaboration of BENEKE. The new fourth edition by BENEKE and JOST[1] is published in two volumes, the first of which, revised by BENEKE, deals with metabolism, and the second volume, prepared by JOST, covers the field of growth and movement.

There has been no change in organization of the first volume, which contains nineteen chapters with the same chapter headings as the first nineteen lectures of the previous edition. The second volume, however, shows some notable changes in organization of contents. The eleven lectures of part II of the former edition have been replaced by three chapters, the first of which introduces the problems of growth of cells and organs, and methods of measuring growth. The second chapter deals with the external and internal factors which cause and modify or condition the rate of growth. The third chapter considers the whole developmental process of plants, from the resting seed or bud to senescence and death. The twelve lectures on movement, part III of the older edition, are replaced by four chapters, dealing with hygroscopic bursting and throwing movements, tropisms, nasties, and locomotor movements, or taxies. These changes of organization in the second volume make a decided improvement from the standpoint of mere organization.

The revision seems to the reviewer to be fairly adequate from the European point of view, their literature having been well summarized. The American plant physiologists, however, will find it necessary to summarize and incorporate the advances made here mainly from the original sources. As the senior author remarks: "So lege ich auch ohne Gefühl der Befriedigung die Feder nieder in dem Bewusstsein dass vieles besser hätte werden können." Difficulties have no doubt lain in the way of a thorough analysis of our contributions to plant physiology; but this must not continue to be an excuse for failure to internationalize the results of scientific investigation. This new edition will be desired by every student of plant physiology, regardless of the obvious shortcomings with reference to American literature.—C. A. SHULL.

[1] BENEKE, WILHELM, and JOST, LUDWIG, Pflanzenphysiologie. Two vols. 8vo. viii+441; and viii+477. Jena. Fischer. 1923.

Standardized plant names

A volume under this name has just been published,[2] which is the result of the cooperative efforts of more than a dozen of the leading horticultural societies of America, and has for its object the adoption of a uniform nomenclature of the scientific and common names of plants cultivated in the United States. The scientific names approved are almost entirely in accord with the international rules of nomenclature. In standardizing the common names, it has been found necessary not only to select from those already in use, but also to bestow a number of new names, and even then some plants are without any common designation. For these the public are invited to make suggestions. The adopted names are declared standard for not less than a five-year period.

The purpose of the work is a most commendable one, and on the whole the results seem to be excellent. The volume is convenient, both in size and in the alphabetical arrangement of its contents, with different faced types for scientific, common, and synonymous designations. Plants with recognized Latin and common names appear in the list under each name. A large number of horticultural varieties is included.—GEO. D. FULLER.

Micro-organisms of soil

RUSSELL and co-workers[3] have published an important book dealing with the micro-organisms of the soil. It is one of the Rothamsted monographs. The organisms included are bacteria, protozoa, algae, fungi, and invertebrate fauna (other than protozoa). Each group is dealt with by the person in charge of the particular department at Rothamsted. In a beginning chapter RUSSELL develops the idea of a soil population, considering the historical features and furnishing the background for the later chapters. In a final chapter he considers the chemical activities of these organisms, and relates them to the growing plant. The book constitutes a good critical summary of what we know concerning the micro-organisms of the soil. At the same time, each chapter is teeming with the many problems that remain to be solved in this important and almost virgin field of investigation. RUSSELL and his associates have done a real service to the general biologist as well as to the specialist in plant physiology and agriculture in publishing this book.—S. V. EATON.

A textbook on botany

SINNOTT[4] has published an attractive textbook of botany which is the outgrowth of teaching college freshmen. The mechanical execution is excellent,

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[2] OLMSTEAD, F. L., COVILLE, F. V., and KELSEY, H. P., Standardized plane names: a catalogue of approved scientific and common names of plants in American commerce. 8vo. xvi+546. Salem, Mass. Amer. Joint Comm. on Horticultural Nomenclature. 1924.

[3] RUSSELL, SIR E. JOHN, and others, The micro-organisms of the soil, pp. vii+188, figs. 24. Longmans, Green & Co. 1923.

[4] SINNOTT, E. W., Botany, principles and problems. Pp. xix+385, New York: McGraw Hill Book Co. 1923.

the figures clear and to the point. The style is lucid, and the subject matter well selected. After an introductory survey, the author discusses soil, the structure and function of root, leaf, and stem. Metabolism and growth are the next chapter topics; then the plant, its environment, reproduction, heredity, variation, and evolution. The last five chapters are devoted to a survey of the plant kingdom. At the conclusion of each chapter there is a series of questions for thought and discussion, 816 questions in all, and also a list of 144 problems. The latter require the study of material outside of the book; the former may be answered from the information the book imparts. These questions and problems should serve as a stimulating help to the teacher.—E. R. DOWNING.

NOTES FOR STUDENTS

Taxonomic notes.—DOMIN, of Prague, has published a long delayed paper on additions to the flora of Western Australia. It was presented to a scientific society in 1917, but publication was much delayed by "difficulties involved in publication during the war and after it." The publication (1923) of 123 pages includes numerous species, many of which are new, and among them a new genus (*Nemcia*) of Compositae.

Miss OTTLEY[5] has published a very complete and well illustrated revision of the Californian species of *Lotus*, recognizing 29 species. It is interesting to note that 24 of these species are referred to GREENE, and also that the genus *Hosackia* is included in *Lotus*.

RIDLEY,[6] in preparing the Euphorbiaceae for the *Flora of the Malay Peninsula*, has discovered 21 new species, representing 14 genera, one of the genera (*Actephilopsis*) being new.

WILSON[7] has published a revision of *Dicoma* (Compositae), a genus of tropical and southern Africa and the East Indies, recognizing 34 species, only one of which is described as new. The fact that this genus is credited with only 13 species in DURAND'S *Index Generum Phanerogamorum* of 1888 illustrates the development of knowledge of the African flora.

BRACKETT[8] has published a revision of the American species of *Hypoxis*, recognizing 15 species, 4 of which are described as new. This genus occurs mostly in the southern hemisphere.

PEARSON[9] has published an account of collections of New Zealand Hepaticae, made by SETCHELL in 1904, which includes descriptions of 15 new species distributed among 12 genera.

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[5] OTTLEY, ALICE M., A revision of the Californian species of *Lotus*. Univ. Calif. Publ. Bot. **10**:189–305. *pls. 61–82.* maps 10. 1923.

[6] RIDLEY, H. N., New Euphorbiaceae from the Malay Peninsula. Bull. Kew Gardens. no. 10. 360–369. 1923.

[7] WILSON, F. C., Revision of the genus *Dicoma*. Bull. Kew Gardens. no. 10. 377–388. 1923.

[8] BRACKETT, A., Contrib. Gray Herb. N.S. 69. pp. 120–163. *figs. 17.* 1923.

[9] PEARSON, W. H., Univ. Calif. Publ. Bot. **10**:307–392. *pls. 83–109.* 1923.

JOHNSTON[10] has published a second paper on Boraginaceae, which is a synopsis of the American native and immigrant species of the subfamily Boraginoideae. It includes 31 genera, one of which (*Lasiarrhenum*) is new. The largest genus is *Lithospermum* with 32 species, 4 of which are new. There are numerous new varieties and combinations. There is also given a tentative classification of the South American species of *Coldenia*, 8 species being recognized, and a new section (Sphaerocarya) proposed. In the same contribution some "taxonomic records" are published, including 27 new species in various genera.

MUNZ[11] has published a revision of *Nemacladus*, chiefly a Californian genus, assigned by TORREY to the Lobeliaceae, but now included in the Campanulaceae. MUNZ recognizes three species, *N. longiflorus*, *N. ramosissimus* (with two varieties), and *N. rigidus* (with five varieties).

ROBINSON,[12] in continuing his studies of the tropical American Eupatorieae, has described 35 new species, 27 of which belong to *Eupatorium*.

JOHNSTON[13] has described new genera of Euphorbiaceae (*Halliophytum*) and Compositae (*Eremonanus*) from California, in addition to numerous new species.

RYDBERG,[14] in his investigation of the genera of North American Fabaceae, has begun the publication of his results in reference to the tribe Galegeae. He recognizes 11 subtribes, 5 of which are presented in the present contribution, including 12 genera, one of which (*Daubentoniopsis*) is described as new, based on *Aeschynomene longifolia* Cav.—J. M. C.

Temperature and flowering.—A study of the blooming habits of *Carnegiea gigantea* has been made by JOHNSON,[15] who finds that the flowers on the east side of the crowns develop more rapidly and open earlier than those situated on other parts of the crown, and that they are more numerous on the east half of the plant. The various factors which might cause these differences in distribution and rate of development are considered, with the conclusion that temperature differences in the tissues of the crown are responsible for the observed facts. The early insolation of the east side of the plant brings about a heating effect which produces a temperature about 2° C. higher in the tissues

[10] JOHNSTON, I. M., Contrib. Gray Herb. N.S. 70. pp. 1–92. 1924.

[11] MUNZ, P. A., A revision of the genus *Nemacladus* (Campanulaceae). Amer. Jour. Bot. **11**:233–248. 1924.

[12] ROBINSON, B. L., Records preliminary to a general treatment of the Eupatorieae. III. Contrib. Gray Herb. no. 68. 1–43. 1923.

[13] JOHNSTON, I. M., Diagnoses and notes relating to the Spermatophytes chiefly of North America. Contrib. Gray Herb. no. 68. 80–104. 1923.

[14] RYDBERG, P. A., Genera of North American Fabaceae. I. Tribe Galegeae. Amer. Jour. Bot. **10**:485–498. 1923.

[15] JOHNSON, D. S., The influence of insolation on the distribution and on the developmental sequence of the flowers of the giant cactus of Arizona. Ecology **5**:70–82. 1924.

of that side. The temperature difference reaches a maximum at about ten or eleven o'clock, but persists as actually higher in temperature than other parts of the crown until about three in the afternoon. After that time the west side may be warmer than the other parts, but its period of high temperature is much briefer than that of the east side. This higher average temperature of the eastern and southeastern parts of the crown is believed to be nearer the optimum temperature for growth of the cactus buds and flowers, and more favorable to a high percentage of bud development.

Evidence is accumulating to show that temperature is a very potent influence in the blooming behavior of plants, and that photoperiodic responses may be very greatly modified by temperature effects. This is probably associated with the internal nutritive conditions of the tissues, flowering depending upon some sort of balance of nutritive relations which is upset by the independent variation of the factors which determine those nutritive conditions, mainly light and temperature.—C. A. SHULL.

Permeability.—In a series of papers, just concluded, STILES[16] has summarized the results of workers in the field of permeability, indicating in a critical manner the chief problems. A discussion of the complexity of the system involved, and the inadequacy of our knowledge of it, serve as an introduction. It is believed that the cell wall is a part of that system. Physico-chemical relations are discussed under such chapter headings as Surface phenomena, Diffusion, Permeability of membranes, Osmotic pressure. In a consideration of the internal conditions which influence the passage of water through the cell wall and protoplasm, the simple osmotic view of the cell is emphasized and its inadequacy shown. Particular emphasis is laid on exact measurements of the effects of temperature, and the composition of the external medium. The chief problem in understanding the passage of dissolved salts is the perfection of quantitative methods for determining intake and outgo. Few reliable data are available. The author feels that no theory of permeability has sufficient quantitative data to support it as yet, and the real usefulness of theories is stimulative. The main problem in the field of permeability is to get sufficient quantitative data that the laws governing the intake of substances from the external surroundings, passage outward from the cell, and translocation from cell to cell within the organism may be formulated. A complete bibliography is included. These papers are so valuable that they should be made available to physiologists in the form of a reprint.—W. B. DAVIS.

Phosphates in relation to algal plankton.—Using colorimetric methods, ATKINS[17] has studied the phosphate content of various salt and fresh waters. He

[16] STILES, W., Permeability. New Phytol. **20**:45–55, 93–106, 137–149, 185–194. 1921; **21**:1–14, 49–65, 140–162, 169–209, 233–251. 1922; **22**:1–29, 72–94, 128–149. 204–224, 239–280. 1923.

[17] ATKINS, W. R. G., The phosphate content of fresh and salt waters in its relationship to the growth of the algal plankton Jour. Marine Biol. Assn. **13**:119–150. 1923.

finds that the phosphate content of salt waters decreases from March to July, when it may be zero. In the case of certain fresh water ponds, the amount of phosphorus present is almost zero by April, and continues low throughout the summer. To explain this decrease in the phosphorus content, the hypothesis is advanced that it is due to an increase in algal plankton, the algae using the phosphorus in the building of body tissues. In support of this hypothesis, it was found that in the case of pure laboratory cultures of diatoms, the phosphate content decreased as the number of diatoms increased. Also, sea water insolated in the laboratory showed a gradually decreasing amount of phosphorus present. Data as to the amount of phosphorus used by diatoms and the phosphate content of sea water are used to estimate the theoretically possible algal plankton crop, and also the possible fish production. Many algae are eaten by animals, and so the actual number of algae present is always far below the possible number. ATKINS' work shows an interesting correlation between the phosphorus content of fresh and salt waters and the number of algae present.—S. V. EATON.

Effect of hydroxyl ion on growth.—There have been many contributions in recent years on the effect of the hydrogen ion on growth, and the field has been somewhat overworked. Not so much attention has been given to the hydroxyl ion. REED and HAAS[18] report the results of experiments concerning the effect of the hydroxyl ion on the growth of walnut roots. They consider the question as to whether the sensitivity of walnuts to alkaline conditions is due to the hydroxyl ion or to the lack of calcium. Their results indicate that the latter is the case. The roots were quickly injured in alkaline nutrient solutions from which calcium was omitted. On the other hand, the roots remained healthy in a calcium hydrate solution of P_H 9.0 or higher. Roots injured in alkaline calcium-free nutrient solutions quickly recovered when transferred to solutions containing calcium, while healthy roots transferred from a calcium hydrate solution to an alkaline solution lacking calcium were soon injured. Such experiments indicate that the bad effects of alkaline conditions on walnut roots are not due to the hydroxyl ion as such, but to the fact that in these alkaline conditions the calcium is precipitated from solution. The paper is well illustrated by text figures.—S. V. EATON.

Vegetation of the Carpathians.—In a recent publication, DOMIN[19] has outlined the zonation of vegetation in the Western Carpathians, which in general rise from a lowland of oak or mixed deciduous forest. Above this the usual zonation is: (1) a submontane zone with the upward extension of the lowland

[18] REED, H. S., and HAAS, A. R. C., The effect of the hydroxyl ion concentration on the growth of walnut roots. Amer. Jour. Bot. 11:78–84. 1924.

[19] DOMIN, K., A phytogeographical outline of the zonal division of the Western Carpathians, besides some general remarks on the main forest trees. Publ. Faculte des Sciences Univ. Charles. Prague. pp. 43. 1923.

forest with some admixture of beech, fir, and pine; (2) a montane beech zone; (3) an upper montane spruce zone with an upper limit ranging from 1350 to 1500 m.; (4) a subalpine zone of dwarf pine (*Pinus montana*) up to 1500 to 2000 m.; and (5) an alpine zone. Not the least interesting and important part of the study consists of an analysis of the factors which cause variations in the limits of these zones or even their inversion. For example, in deep valleys the spruce may occupy the damp, cool, lower portions, and be surmounted on the drier sunnier slopes by a beech zone, or either the beech or the spruce may occupy both the lower and the upper montane zones. Emphasis also is given to the variations in the altitudinal limits of the zones due to soil, exposure, and other agencies.—GEO. D. FULLER.

North American flora.—The fourth part of volume 25 contains the completion of Geraniales, the Meliaceae by PERCY WILSON and the Trigoniaceae by P. C. STANDLEY; and also the beginning of Polygalales, the Vochyaceae by P. C. STANDLEY and the first instalment of Polygalaceae by D. F. BLAKE. In Meliaceae 7 genera are recognized, including 88 species, the large genera being *Gaurea* and *Trichilia*, each with 33 species. The family Trigoniaceae is represented by a single genus with 2 species, and Vochyaceae includes a single genus with 4 species. The family Polygalaceae is begun with *Polygala*, in which 179 species are recognized, 43 being presented in the present part, 3 of which are described as new.—J. M. C.

Anatomy of Selaginella.—Miss STEEL[20] has published an interesting account of the anatomy of *Selaginella uliginosa*, a common species of Eastern Australia. The shoot has the radial type of vascular cylinder, which is now recognized as the most primitive type of stem cylinder, persistent chiefly in roots. The rhizome is solenostelic, and the root protostelic, with only one group of protoxylem. The general conclusion is that *S. uliginosa* is one of the more primitive species of the genus. The combination of heterospory with a primitive vascular situation is a combination which makes *Selaginella* an unusually interesting type.—J. M. C.

The strobilus theory.—PARKIN[21] has restated and amplified the theory of the origin of angiosperms proposed by the late Dr. NEWELL ARBER and himself in 1907. He assembles evidence to show that Ranales contain the families with least modified flowers (really strobili), from which all other flowers have been derived by reduction and modification. This discards the Engler series in regard to Amentiferae as the most primitive. The Ranales, in turn, are regarded as related in origin to such Gymnosperms as the Bennettitales, at least in common origin from the "Pteridosperms." The details of data and conclusions are interesting, although not always convincing.—J. M. C.

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[20] STEEL, JESSIE K., Anatomical features of the mature sporophyte of *Selaginella uliginosa*. Proc. Linn. Soc. New South Wales **48**:287–300. 1923.

[21] PARKIN, J., The strobilus theory of angiospermous descent. Proc. Linn. Soc. London. pp. 51–64. 1923.

Hydrogen ion determination of tissues.—A method of determining the hydrogen ion concentration of tissues colorometrically is described by ATKINS,[22] who applies the indicators directly to sections or to the crushed tissues. Attention is called to the usefulness of diethyl red in regions of acidity where methyl red and brom cresol purple are yellowish, and hard to distinguish from tissue colors when applied directly. Many tissues lie in this range. It is also pointed out that methyl orange is useful in more acid regions where brom phenol blue is yellow.—W. B. DAVIS.

Evolution of herbaceous angiosperms.—SINNOTT and BAILEY[23] have felt the necessity of restating their conclusions in reference to the evolution of herbaceous angiosperms from arborescent or fruticose ancestors, published in 1914.[24] These conclusions have been criticized since that time in such a way that the authors have endeavored "to clarify the real points at issue," and thus correct what seems to be a misunderstanding.—J. M. C.

Embryo sac of Oenothera rubrinervis.—O'NEAL[25] has investigated the development of the embryo sac of *Oenothera rubrinervis*, and in addition to the usual events records the following facts: the micropylar megaspore usually becomes the functional one; the mature sac contains but four nuclei; fertilization occurs about thirty-six hours after pollination and is probably "single."—J. M. C.

Embryogeny.—SOUÈGES,[26] in continuation of his numerous studies of embryogeny, has published the usual very detailed and well illustrated accounts of embryo development in *Myosotis hispida* and *Geum urbanum*.—J. M. C.

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[22] ATKINS, W. R. G., The hydrogen ion concentration of plant cells. Notes Bot. School Trinity College, Dublin **3**:178–198. 1922.

[23] SINNOTT, E. W., and BAILEY, I. W., The significance of the "foliar ray" in the evolution of herbaceous angiosperms. Ann. Botany **36**:523–533. *pls. 18, 19. fig. 1.* 1922.

[24] Review in BOT. GAZ. **60**:247. 1915.

[25] O'NEAL, C. E., A study of the embryo sac development and accompanying phenomena in *Oenothera rubrinervis*. Bull. Torr. Bot. Club **50**:133–146. *pls. 5, 6.* 1923.

[26] SOUÈGES, R., Développement de l'embryon chez le *Myosotis hispida* Schlecht. Bull. Soc. Bot. France. Ser. IV. **23**:385–401. 1923.

———, Développement de l'embryon chez le *Geum urbanum* L. Ibid. 645–660. 1923.